

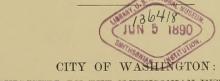
# SMITHSONIAN

# CONTRIBUTIONS TO KNOWLEDGE.

VOL. XXVI.



"EVERY MAN IS A VALUABLE MEMBER OF SOCIETY, WHO, BY HIS OBSERVATIONS, RESEARCHES, AND EXPERIMENTS, PROCURES KNOWLEDGE FOR MEN."—SMITHSON.



PUBLISHED BY THE SMITHSONIAN INSTITUTION. 1890.



# ADVERTISEMENT.

This volume forms the twenty-sixth of a series, composed of original memoirs on different branches of knowledge, published at the expense, and under the direction, of the Smithsonian Institution. The publication of this series forms part of a general plan adopted for carrying into effect the benevolent intentions of JAMES SMITHSON, Esq., of England. This gentleman left his property in trust to the United States of America, to found, at Washington, an institution which should bear his own name, and have for its objects the "increase and diffusion of knowledge among men." This trust was accepted by the Government of the United States, and an Act of Congress was passed August 10, 1846, constituting the President and the other principal executive officers of the general government, the Chief Justice of the Supreme Court, the Mayor of Washington, and such other persons as they might elect honorary members, an establishment under the name of the "Smithsonian INSTITUTION FOR THE INCREASE AND DIFFUSION OF KNOWLEDGE AMONG MEN." The members and honorary members of this establishment are to hold stated and special meetings for the supervision of the affairs of the Institution, and for the advice and instruction of a Board of Regents, to whom the financial and other affairs are intrusted.

The Board of Regents consists of two members ex officio of the establishment, namely, the Vice-President of the United States and the Chief Justice of the Supreme Court, together with twelve other members, three of whom are appointed by the Senate from its own body, three by the House of Representatives from its members, and six persons appointed by a joint resolution of both houses. To this Board is given the power of electing a Secretary and other officers, for conducting the active operations of the Institution.

To carry into effect the purposes of the testator, the plan of organization should evidently embrace two objects: one, the increase of knowledge by the addition of new truths to the existing stock; the other, the diffusion of knowledge, thus increased, among men. No restriction is made in favor of any kind of knowledge; and, hence, each branch is entitled to, and should receive, a share of attention.

<sup>&</sup>lt;sup>1</sup> This office has been abolished.

The Act of Congress, establishing the Institution, directs, as a part of the plan of organization, the formation of a Library, a Museum, and a Gallery of Art, together with provisions for physical research and popular lectures, while it leaves to the Regents the power of adopting such other parts of an organization as they may deem best suited to promote the objects of the bequest.

After much deliberation, the Regents resolved to divide the annual income into two parts—one part to be devoted to the increase and diffusion of knowledge by means of original research and publications—the other part of the income to be applied in accordance with the requirements of the Act of Congress, to the gradual formation of a Library, a Museum, and a Gallery of Art.

The following are the details of the parts of the general plan of organization provisionally adopted at the meeting of the Regents, Dec. 8, 1847.

#### DETAILS OF THE FIRST PART OF THE PLAN.

- I. To increase Knowledge.—It is proposed to stimulate research, by offering rewards for original memoirs on all subjects of investigation.
- 1. The memoirs thus obtained, to be published in a series of volumes, in a quarto form, and entitled "Smithsonian Contributions to Knowledge."
- 2. No memoir, on subjects of physical science, to be accepted for publication, which does not furnish a positive addition to human knowledge, resting on original research; and all unverified speculations to be rejected.
- 3. Each memoir presented to the Institution, to be submitted for examination to a commission of persons of reputation for learning in the branch to which the memoir pertains; and to be accepted for publication only in case the report of this commission is favorable.
- 4. The commission to be chosen by the officers of the Institution, and the name of the author, as far as practicable, concealed, unless a favorable decision be made.
- 5. The volumes of the memoirs to be exchanged for the Transactions of literary and scientific societies, and copies to be given to all the colleges, and principal libraries, in this country. One part of the remaining copies may be offered for sale; and the other carefully preserved, to form complete sets of the work, to supply the demand from new institutions.
- 6. An abstract, or popular account, of the contents of these memoirs to be given to the public, through the annual report of the Regents to Congress.

- II. To increase Knowledge.—It is also proposed to appropriate a portion of the income, annually, to special objects of research, under the direction of suitable persons.
- 1. The objects, and the amount appropriated, to be recommended by counsellors of the Institution.
- 2. Appropriations in different years to different objects; so that, in course of time, each branch of knowledge may receive a share.
- 3. The results obtained from these appropriations to be published, with the memoirs before mentioned, in the volumes of the Smithsonian Contributions to Knowledge.
  - 4. Examples of objects for which appropriations may be made:—
- (1.) System of extended meteorological observations for solving the problem of American storms.
- (2.) Explorations in descriptive natural history, and geological, mathematical, and topographical surveys, to collect material for the formation of a Physical Atlas of the United States.
- (3.) Solution of experimental problems, such as a new determination of the weight of the earth, of the velocity of electricity, and of light; chemical analyses of soils and plants; collection and publication of articles of science, accumulated in the offices of Government.
- (4.) Institution of statistical inquiries with reference to physical, moral, and political subjects.
- (5.) Historical researches, and accurate surveys of places celebrated in American history.
- (6.) Ethnological researches, particularly with reference to the different races of men in North America; also explorations, and accurate surveys, of the mounds and other remains of the ancient people of our country.
- I. To diffuse Knowledge.—It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge not strictly professional.
- 1. Some of these reports may be published annually, others at longer intervals, as the income of the Institution or the changes in the branches of knowledge may indicate.
- 2. The reports are to be prepared by collaborators, eminent in the different branches of knowledge.

- 3. Each collaborator to be furnished with the journals and publications, domestic and foreign, necessary to the compilation of his report; to be paid a certain sum for his labors, and to be named on the title-page of the report.
- 4. The reports to be published in separate parts, so that persons interested in a particular branch, can procure the parts relating to it, without purchasing the whole.
- 5. These reports may be presented to Congress, for partial distribution, the remaining copies to be given to literary and scientific institutions, and sold to individuals for a moderate price.

The following are some of the subjects which may be embraced in the reports:—

#### I. PHYSICAL CLASS.

- 1. Physics, including astronomy, natural philosophy, chemistry, and meteorology.
- 2. Natural history, including botany, zoology, geology, &c
- 3. Agriculture.
- 4. Application of science to arts.

#### II. MORAL AND POLITICAL CLASS.

- 5. Ethnology, including particular history, comparative philology, antiquities, &c.
- 6. Statistics and political economy.
- 7. Mental and moral philosophy.
- 8. A survey of the political events of the world; penal reform, &c.

#### III. LITERATURE AND THE FINE ARTS.

- 9. Modern literature.
- 10. The fine arts, and their application to the useful arts.
- 11. Bibliography.
- 12. Obituary notices of distinguished individuals.

# II. To diffuse Knowledge.—It is proposed to publish occasionally separate treatises on subjects of general interest.

- 1. These treatises may occasionally consist of valuable memoirs translated from foreign languages, or of articles prepared under the direction of the Institution, or procured by offering premiums for the best exposition of a given subject.
- 2. The treatises to be submitted to a commission of competent judges, previous to their publication.

#### DETAILS OF THE SECOND PART OF THE PLAN OF ORGANIZATION.

This part contemplates the formation of a Library, a Museum, and a Gallery of Art.

- 1. To carry out the plan before described, a library will be required, consisting, 1st, of a complete collection of the transactions and proceedings of all the learned societies of the world; 2d, of the more important current periodical publications, and other works necessary in preparing the periodical reports.
- 2. The Institution should make special collections, particularly of objects to verify its own publications. Also a collection of instruments of research in all branches of experimental science.
- 3. With reference to the collection of books, other than those mentioned above, catalogues of all the different libraries in the United States should be procured, in order that the valuable books first purchased may be such as are not to be found elsewhere in the United States.
- 4. Also catalogues of memoirs, and of books in foreign libraries, and other materials, should be collected, for rendering the Institution a centre of bibliographical knowledge, whence the student may be directed to any work-which he may require.
- 5. It is believed that the collections in natural history will increase by donation, as rapidly as the income of the Institution can make provision for their reception; and, therefore, it will seldom be necessary to purchase any article of this kind.
- 6. Attempts should be made to procure for the gallery of art, casts of the most celebrated articles of ancient and modern sculpture.
- 7. The arts may be encouraged by providing a room, free of expense, for the exhibition of the objects of the Art-Union, and other similar societies.
- 8. A small appropriation should annually be made for models of antiquity, such as those of the remains of ancient temples, &c.
- 9. The Secretary and his assistants, during the session of Congress, will be required to illustrate new discoveries in science, and to exhibit new objects of art; distinguished individuals should also be invited to give lectures on subjects of general interest.

In accordance with the rules adopted in the programme of organization, each memoir in this volume has been favorably reported on by a Commission appointed for its examination. It is however impossible, in most cases, to verify the statements of an author; and, therefore, neither the Commission nor the Institution can be responsible for more than the general character of a memoir.

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# RESEARCHES

UPON THE

# VENOMS OF POISONOUS SERPENTS.

 $\mathbf{B}\mathbf{Y}$ 

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[ACCEPTED FOR PUBLICATION, MAY, 1885.]

WASHINGTON: PUBLISHED BY THE SMITHSONIAN INSTITUTION. 1886.

### COMMISSION

TO WHICH THIS MEMOIR HAS BEEN REFERRED.

JOHN S. BILLINGS, M. D., HENRY G. BEYER, M. D.

> Spencer F. Baird, Secretary S. I.

### PREFACE.

The authors desire to express their multiple obligations to the Smithsonian Institution. They have to thank the Army Medical Library for the valuable Bibliography appended to this essay. With that to be found in Dr. Weir Mitchell's former essay, it completes the list of such knowledge up to January, 1885. They desire also to thank Her Britannic Majesty's Indian Government for help in securing Indian serpent poisons. Among individuals they owe to no one so deep a debt as to Vincent Richards, Esq., of Goalundo, British India. Without his untiring aid the authors feel that it would have been impossible to have extended their inquiries beyond our native snakes.

The excellent plates were drawn for the most part by Dr. J. Madison Taylor, and thanks are due to Dr. Geo. A. Piersol's skill for the interesting microphotographs of blood-corpuscles attacked by venom. The authors are also indebted to Dr. Guy Hinsdale for having made the tabulated reductions of kymographion tracings.

S. WEIR MITCHELL, EDWARD T. REICHERT.

Physiological Laboratory of the University of Pennsylvania.



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### INTRODUCTION.

A few words of explanatory character in regard to the following essay may not be out of place. From the time of Fontana, 1767, until the able essay of Lucien Bonaparte, in 1843, on the chemistry of venom, there was no paper of moment on serpent poisons. In January, 1861, one of us, S. Weir Mitchell, published a long study of the venom of the *Crotalus durissus*, and in 1868 supplemented it by a shorter contribution, in which he related some recent discoveries of his own, and corrected certain errors of his former paper. These two essays may be considered as constituting with Lucien Bonaparte's the foundation of the later work in this direction, and perhaps as having left the study of venoms in as definite a position as could be gained with the laboratory facilities of 1843 to 1868.

In 1872, the government of India enabled Sir Joseph Fayrer to publish a volume of beautiful plates of the venomous snakes of India, to which was appended also a series of investigations into the toxicology of their poisons. In 1872 the same author and Dr. Lauder Brunton contributed an admirable physiological study of the effects of venoms.<sup>1</sup>

In 1874, Vincent Richards, as chairman of a government commission, published an excellent report on antidotes.

Dr. Wall's² thoughtful and suggestive book appeared in 1883. It is a comparative study of the poisons of the colubrine and viperine serpents of India.

These, with a too brief study of the poison of our copperhead by Dr. Isaac Ott, of Easton, Pennsylvania, sum up all of value which has been added to the physiological literature of this most interesting subject.

Why it has won so few investigators is not far to seek. Even in India, where the appalling loss of life from snake-bites has of late invigorated research, the power and means of government were needed to overcome the obstacles which surround such scientific effort from inception to close. But, if in a land where snakes abound and professional snake-catchers can be had, it is yet not easy to follow this pursuit with success, elsewhere it is a task set about with inconceivable obstacles. The fear of serpents, the rarity of some species, the distances to which they have to be carried, the mortality of caged specimens, and the great cost of

<sup>&</sup>lt;sup>1</sup> Proc. Roy. Soc. 1872, 1873, and 1875.

<sup>&</sup>lt;sup>2</sup> Indian Snake Poisons; their Nature and Effects. A. J. Wall, M.D., F.R.Coll.S., 1883.
1 April, 1886. (1)

purchase and transportation, need only to be mentioned as indicating our own difficulties. What had been done in India, sustained by a government, had to be with us attempted by private individuals, aided by the Smithsonian Institution, without which it would have been impossible to succeed. Our work began in the autumn of 1882, by extended efforts on our part, and that of the Smithsonian, to buy or otherwise get numerous living specimens of the American genera of Thanatophideæ. This quest was kept up by every means our ingenuity could devise, and neither time nor money was spared. We succeeded in obtaining a sufficient number of rattlesnakes, including Crotalus adamanteus and C. durissus. We have had also enough of the Moccasin (Ancistrodon piscivorus). Our wants as regards Ground Rattlesnakes, Copperheads, and Coral-snakes have been less competently supplied, chiefly because these snakes are all small, so that to get enough of their poison for study it was essential to have a great many snakes. We have had in all about two hundred living serpents, and among them some superb specimens, which yielded poison in large quantities. Thus one—C. adamanteus was eight and a half feet long and weighed nearly nineteen pounds. It furnished on one occasion about one and a half drachms of venom.

It was thought desirable by Prof. Baird and ourselves to examine the poisons of Indian serpents. To secure these the Secretary of State appealed to Her Majesty's Indian government in our behalf. A courteous response was returned, and orders given which resulted in our receiving a certain amount of Cobra venom. A more constant and larger supply was due to the generous and untiring kindness of Vincent Richards, Esq., M.R.C.S., of Goalundo, B. I.

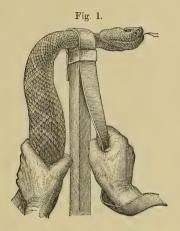
The poison of the *Duboia Russellii*, the Indian viper, we sought in vain to secure. Government aid and private enterprise alike failed to secure a sufficient quantity of the venom of this dreaded reptile. The other Thanatophideæ, of Australia, and South America, still await more careful study, and our preliminary report has already been the means of renewing interest in the chemical aspects of this study in India.

Such of our serpents as were not cared for by the hospitality of the Philadelphia Zoological Garden, were kept in large boxes, about four and a half feet high, covered on top with removable wire network, and well-ventilated through wired openings below. They were of course furnished with water, and if they declined to eat, were fed at intervals, by artificial means, with raw beef chopped fine, and passed down into the belly of the snake through a large glass-tube. Under this treatment the deaths were fewer, and the supply of venom far better. Probably this method could be usefully employed in zoological gardens, where many snakes are lost owing to their indisposition to feed during the early months of captivity.

On all occasions, for forced feeding, or for the purpose of extracting venom, the snakes were caught and held in the snake loop, Fig. 1. This is merely a staff, having a leather strap so arranged that it can be drawn out into a loop in which the serpent's neck is noosed, and so held. With this simple means all risk is avoided, and with it serpents of any size and strength to be met with among our Thanatophideæ can be safely held and easily manipulated.

For whatever reasons the study of snake venoms had not greatly advanced since

the last research of Fayrer and Lauder Brunton until the authors of this paper resumed the work in 1882. One of them (Dr. Mitchell) had long felt that it would be well to revise the toxicology of our American serpents which he had begun in 1858, and as the later English observers had in some points differed from



him, to learn if they or he were correct, or whether the divergence as to results was due to variations in the qualities of the venoms employed. Then too he had become conscious of certain errors in his former researches, and wished to aid in correcting them, and in filling up some of the gaps left in this branch of toxicology by himself and others.

The authors started with a theory long held by Dr. Mitchell that snake venoms are not simple in composition, but composed of two or more poisonous substances, and that in the qualities and quantities of these agents would be found an explanation of the differences between serpent venoms as to power to kill and mode of causing death.

How fertile has been the germinal idea of this research must be judged of by this present essay; which will, we trust, by leading thought and experiment in new directions hasten the day when we shall be able to treat with success the wretched thousands who now perish annually by snake-bite in India and elsewhere.

Some of our earlier results were so soon talked of and even noted in public prints, that it seemed wise for this, and all other reasons, to state what we then knew. This was done in a "Preliminary Report to the United States National Academy of Sciences, in April, 1883." In this brief essay we announced our proofs of the complex nature of snake poisons. The report was incomplete, and in the light of our present more elaborate essay may be seen to contain several erroneous statements.

It is not in the nature of things, that a research along such varied lines as our present volume follows, though extending over several years, should be perfect in detail, or complete for all genera of Thanatophidians. It is our earnest hope that it will be complemented and supplemented by some of the able staff of the British Army Medical Service in the East Indies. There, only, is it possible to find enough serpents, and all the various species which it will be desirable to review toxicologically from the new stand-point which we think we have established.

We have forborne to overload this paper with comments on the later researches of others, and have made the discussion of our own work as brief as was consistent with clearness.

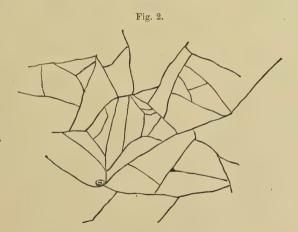
In writing of the various substances contained in venoms, we have given them names which are fairly descriptive, but which, as in the case of the peculiar peptone of Cobra, may perhaps excite criticism. Yet, however unsatisfactory our method of nomenclature may be, any other plan of naming the curious bodies in question would certainly have been even more misleading.

#### CHAPTER I.

## PHYSICAL CHARACTERISTICS OF VENOM.

Physical Characteristics of Venom.—All serpent venoms are more or less alike in appearance when fresh. They are fluids varying in color from the palest amber tint to a deep yellow. Dr. Wall describes the Cobra venom as being occasionally colorless. This peculiarity we have never seen in the fresh poison of any of our serpents, except once in the coral snake; nor can the venom of one kind of snake be distinguished with certainty by any physical peculiarity from that of any other, however remote they may be in the scale of being.

When a fluid venom is allowed to dry slowly it presents no specific distinctive appearances. If desiccated too rapidly, it may look a little more gray and opaque than is common, but usually it dries into a beautifully cracked mass, deceptively like an aggregation of crystals, and which is well represented in Fig. 2.



In this state it is in solid yellow particles, very fragile, bright yellow, transparent or translucent, and seemingly indestructible by time, since the dried venom of the rattlesnake, for twenty-two years in Dr. Mitchell's possession, proved as poisonous as that removed yesterday. It is equally unaltered by solution in glycerin, which keeps it permanently in unchanged toxic force, as we shall here-

after point out. Neither does it appear to be injured when dry by mingling it with pure alcohol. In fact any of these three means, desiccation, glycerin, or alcohol, preserves it well.

When fresh venom of any serpent is examined with the microscope it often presents a variety of floating bodies which seem to be much alike in all cases, and are very well shown in the plates of Dr. Mitchell's former paper and in Vincent Richards's reports. In healthy serpents, but lately caged, there are fewest of these solid ingredients, as has been noticed by Richards, by Wall, and by S. Weir Mitchell. The question of the toxicity of these suspended solids has again drawn our attention to them, and we have had yet more careful and repeated microscopic examinations made by Prof. Formad. He found, like other observers, that the venom of the more vigorous snakes has the least visible solid matter; but, as in the use of the fang, the mucus and floating solids of the mouth must be considered, and, as in collecting venom from the snake, more or less of the mouth fluids mingle with the venom, it was thought well to reconsider the nature of the floating solids from the point of view of toxic activity. For the better study of the solids found in venoms we examined numerous specimens, and placed many of these in the hands of Prof. Formad, from whose notes we select the following observations:—

A drop of fresh venom, taken directly from the Crotalus adamanteus, was examined with a  $\frac{1}{12}$  Zeiss, homog, immersion lens; amplification 800 diameters. The most striking appearance which first meets the eye is a granular material scattered about in masses of various size and shapes, resembling those formed by bacteria. There are also seen, in some cases, a few oval nucleated red blood-corpuscles, some leucocytes resembling salivary corpuscles, and others corresponding to ordinary white blood-corpuscles, the latter cells in an active state of amæboid motion. There were also observed several club-shaped epithelial cells covered with fine granular material.

The granular matter first mentioned, and which seems to form the main solid constituent of the venom, consists of two elements: Larger granules of an animal or albuminous character, and a fine granular material of vegetable nature. The albuminoid material is made up of minute particles ovoid, or somewhat irregularly angular in shape, measuring about  $\frac{1}{10000}$  of an inch in their longest diameters. These ovoid particles are grouped side by side, from two to twenty in each collection, and are arranged so as to form single or double rows, or more often aggregated into irregularly shaped clusters, which vary in size from  $\frac{1}{500}$  to  $\frac{1}{5000}$  of an inch; the smaller masses predominating. The particles just described are colorless, refracting, and in general give the impression of bacteria. They are, however, distinguished from the latter in that they do not multiply in cultures, or respond to the aniline dye test for bacteria.

There are usually numerous bacteria in perfectly fresh venom. All the smaller particles and granular material are micrococci, measuring on an average  $\frac{1}{40000}$  of an inch in diameter, are perfectly round or somewhat ovoid, and occurring singly,

<sup>&</sup>lt;sup>1</sup> Dr. Mitchell possessed a glycerin solution which was toxic after twenty years.

in pairs, or in zooglea masses. They are less refracting, and paler than the albuminoid particles described above, and respond promptly to the usual tests for bacteria, viz: They multiply rapidly and absorb well the aniline dyes, thus forming a marked contrast side by side with the animal granular material, which was readily discolored under the influence of acid.

The epithelial cells seen in the venom are, as a rule, few in number, are squamous or club-shaped, and in size not exceeding that of the red blood-corpuscle of the serpent. Leucocytes are also few in number, and, as well as the epithelium, are mostly covered with micrococci. A few of the white blood-corpuscles do not appear to contain micrococci, and in fresh venom, especially upon the warming stage, exhibit a quite active amœboid motion. The venom of the moccasin presents the same appearances.

If fresh venom stands but a short time exposed to the air the micrococci multiply with remarkable rapidity, forming large, pale, motionless clouds; but, in addition, multitudes of movable bacteria (the *Bacterium termo* and a bacillus—probably *Bacillus subtilis*) gradually make their appearance.<sup>1</sup>

The globulous masses, above described, may be collected by filtration, but as this is often a difficult or even an impossible process with a fluid as viscous as pure venom, and, as much is lost in the filter, another method was devised, and thereafter frequently used by us as an assistance in venom analysis. A tube, about 5 millimetres wide and 200 to 400 m.m. long, has a bulb blown on it midway, or at the top, and is then closed above in the blowpipe flame, and strongly heated throughout. While hot, the lower end drawn to a point, is in like manner sealed. After being cooled the tip is broken within fresh venom, which is forced up into the tube by atmospheric pressure. The end of the tube is then once more adroitly sealed in the flame.

Thus prepared the tube is suspended, so that the solids of all forms settle in a few days, while for this time, at least, the venom undergoes no such putrefactive change as is inevitable when it is exposed to the air at our ordinary spring or summer temperatures.

The solids, thus collected below, are easily separable from the supernatant venom by breaking off the two ends of the tube and allowing the precipitate to escape, with a minimum amount of liquid, from which washing in water easily separates them.

The physical appearances of the venoms of the moccasin or of the rattlesnake, thus seeluded from the air in these partial vacuum tubes, undergo some curious changes of much interest.

The yellow coloring matter disappears from below upwards, and at last is seen only at the top, where the venom is in contact with the small amount of air left in the tube. At first, this change was presumed to be simply the rising of a pigment of lesser gravity. But it was noticed that the layer of yellow was of no deeper tint in its lessened bulk than when diffused. The fluid below it was left as

<sup>&</sup>lt;sup>1</sup> Fresh venom, putrefied from long standing, appears to lose at least a portion of its virulence. But this is a point which is open to further observation.

clear and tintless as water; but when re-exposed to the air once more became yellow throughout, within one or two hours.

The yellow pigment of Cobra poison, when the dry poison was dissolved in water, does not rise in the tube or disappear, but remains unaltered. It is desirable to repeat these observations with fresh Cobra venom.

The cause of the disappearance and reappearance of the coloring matter of venom we have not been able to explain to our satisfaction, and it is one of the questions left open for inquiry.

The Specific Gravities of Venoms.—The specific gravity of the venoms of our own serpents is as follows:—

Crotalus horridus .		۰		1.054
Crotalus atrox .				1.077
Crotalus adamanteus				1.061
Ancistrodon piscivorus				1.032

The specific gravity of Cobra venom is given by Wall at 1.058. As to that of the Indian viper we can find no statement.

The losses of venom on drying were as follows:-

C. adam					25.15 p	er cent.
C. atrox					25.16	"
Ancis, piscivor	us		2		27.42	44

# CHAPTER II.

### THE CHEMISTRY OF VENOMS.

The presence of alkaloids in venom, and especially of the ptomaines, has been suspected, and these bodies have been repeatedly sought for in vain. Gautier is the only chemist we recall who asserts that he found a ptomaine in a venom (Cobra). He does not state his processes, and we have been utterly unable to substantiate his statements. Lest we should in some way have erred in the conduct of this part of our labor, we asked Prof. Wolcott Gibbs to examine Crotalus venom with a view to detection of such a body. As regards this search he makes the following statement:—

"My investigation of rattlesnake venom had for its special object the comparison of the venom with the higher alkaloids. As the quantity of material at my command was small, I was obliged to content myself with the application of the ordinary tests used for the detection of alkaloids, as, for example, phospho-tungstates and phospho-molybdates, iodide of mercury and potassium, etc. etc. In many cases precipitates were obtained, but these were in no case distinctly crystalline. They resembled, on the contrary, the precipitate formed by sodic phospho-tungstate in solutions of albuminates in acetic acid. It seems, therefore, very improbable that the venom contains an alkaloid in the sense in which that term is commonly employed by chemists. On the other hand, it may still be basic in character, even if it be classed with albuminoids, since these are known to combine with platinous cyanide and with salicylic and other acids, exhibiting the properties of weak bases as well as of weak acids."

Venoms are of acid reaction, but when neutralized we have not observed any precipitate in specimens of these poisons.

When venom is taken from the Crotalus or Ancistrodon there is often observed in the clear poison some insoluble whitish, granular matter, which soon settles to the bottom.

The Insoluble Precipitate.—This insoluble matter, which we term the insoluble precipitate, can be collected for examination by allowing the venom to stand in hermetically sealed vertical tubes, as previously described. The precipitate soon settles to the bottom, the clear venom is then carefully drawn off, and the precipitate is repeatedly washed with distilled water and collected; the washing process is repeated until there is no trace of proteid reaction in the wash-water, or, in other words, until all of the soluble portion of the venom has been completely washed from the precipitate.

When examined under the microscope this precipitate consists of irregular

masses of granular matter with epithelial cells and salivary corpuscles, and a few flat crystals resembling cholesterin:

The precipitate gives no proteid reactions with the usual proteid color tests, is insoluble in neutral saline solutions, and in weak or strong acids or alkalies. Boiling seems to render the mixture clearer.

When injected into pigeons this precipitate does not appear to possess any toxic properties.

The Globulins.—If, after the separation of the above insoluble precipitate, the venom be mixed with water and placed in a dialyser over running water it will be found that within a few hours a whitish precipitate will occur within the dialyser, and should dialysis be continued sufficiently long the precipitate will have become deposited in abundance. If the precipitate thus formed be collected on a filter it will be found that all of the coagulable proteids have been thrown down, since the filtrate now yields no coagulum by brief boiling, although it gives a proteid reaction.

The precipitate is now washed from the filter and subjected to repeated washings and decantations with distilled water, until the wash-water gives no proteid reaction. This purified precipitate is found to give reactions peculiar to the globulins; it is insoluble in distilled water, soluble in dilute neutral saline solutions, soluble in dilute acids and alkalies, becomes turbid at about 60° C., and is fully coagulated at a point a little above 70° C.

The filtrate still contains some proteid in solution, since we find, by the usual color and chemical tests, a proteid reaction, although it is observed that no coagulation occurs by momentary boiling. The filtrate is not precipitated by strong or weak mineral acids, by solutions of ferric chloride or cupric sulphate, it is precipitated but not coagulated by absolute alcohol, and if placed in a dialyser it will be found to be readily dialysable. These reactions it will be observed place the proteid which remains in solution in the filtrate among the peptones. But we shall revert to this hereafter.

It will thus be clear that we have separated in venom representatives of two distinct classes of proteids, one of which is insoluble in distilled water and coagulated in solution by boiling, and another which is soluble in distilled water and non-coagulable by brief boiling; the former belonging to the *globulins* and the other to the *peptones*.

The substance, however, which we find belonging to the globulins is a complex body in its composition, since, by appropriate processes, it can be resolved into three distinct principles, each of which is a globulin, but each having some properties different from its fellows. In order to distinguish these principles we have named them water-venom-globulin, copper-venom-globulin, and dialysis-venom-globulin, the names indicating the principal feature of the processes by which they are isolated from each other. As there are some differences in the reactions of similar principles in different species of venoms, we shall at first speak only of the venom of the Crotalus adamanteus.

Water-venom-globulin.—We have already stated that when a solution of the fresh or dried venom in distilled water is allowed to stand for some time, especially if the quantity of water be comparatively large, a whitish precipitate occurs which

settles to the bottom of the glass, leaving in the course of a few hours a perfeetly clear supernatant liquid. If sufficient water has been added at first, the addition of more distilled water to the supernatant liquid will not cause any further precipitate.

The precipitate is now collected and repeatedly washed with distilled water and

decanted until the wash-water yields no proteid reaction.

The following gives the results of some of the many reactions upon the addition of the various reagents used -- 1

```
Decided reactions with the usual proteid tests.
Boiling—causes coagulation.
Sodic chloride (0.75 per cent.)—slightly soluble.
                              )-soluble, forming a turbid solution; the solution is not precipi-
                 10
                                   tated by carbonic acid2 nor by the addition of ether.
                               -boiling the solution causes coagulation.
                               -the solution is precipitated by saturation with sodic chloride.
```

Carbonic acid1-soluble.

Sodic carbonate—very soluble; solution not precipitated by carbonic acid.

Hydrochloric acid (0 4 per cent.)-very soluble. Metaphosphoric acid-insoluble. Orthophosphoric acid—dissolves. Sodic metaphosphate-insoluble. Sodic orthophosphate-very soluble. Potassic sulphate-very soluble. Calcic chloride-very soluble. Acetic acid (5 per cent.)-very soluble. Acetic acid (glacial)-very soluble.

Coagulation occurs at about 64-73° C.

Since this body is precipitated by saturation with sodic chloride, and dissolves with difficulty in a 0.75 per cent. solution of sodic chloride, it seems more akin to myosin than other of the globulins.

The Copper-venom-globulin.—After the separation of the water-venom-globulin the filtrate gives well-marked proteid reactions and decided coagulation by boiling. If now a few drops of cupric sulphate (10 per cent.) be cautiously added a second precipitate will occur, and which can be separated as in the previous instance. In adding the cupric sulphate great caution must be exercised lest too much be added with the result of a complete or partial re-solution of the precipitate.

The precipitate is sometimes comparatively slight at first, increasing upon standing, and complete within about twenty-four hours. The clear filtrate should give no precipitate after the addition of a small amount of the copper solution and after standing twenty-four hours longer.

<sup>&</sup>lt;sup>1</sup> In all of these reactions with the globulins, unless otherwise apparent, about 1 c. c. of the suspended globulin in distilled water was placed in a small test-tube, and from one to two drops of standard laboratory solutions of reagents were allowed to run down the inside of the tube.

We have made a large number of tests with various reagents, and from this number have selected only such as will serve us some purpose in distinguishing these different bodies.

<sup>&</sup>lt;sup>2</sup> Where carbonic acid is used in these tests we have reference to the super-saturated carbonic acid water (soda water) of commerce.

The precipitate thus obtained is washed as in the preparation of the watervenom-globulin, and when thus purified it does not give any color reaction with the ammonia or the ferrocyanide and acetic-acid tests for copper, and therefore cannot be regarded as a salt of this metal.

The copper-venom-globulin gives the following reactions:—

Decided reactions with the usual proteid tests. Sodic chloride (0 75 per cent.)—insoluble.

(10 ")—insoluble.

—the addition of crystals of sodic chloride seems to dissolve it slightly; this solution is cleared somewhat by boiling; the same effect by boiling the suspended mixture; the clearing is no doubt the result of the formation of coagula.

Carbonic acid-insoluble.

Sodic carbonate—very soluble, forming a beautiful clear solution; boiling has no effect; the solution is precipitated by carbonic acid.

Hydrochloric acid (0.4 per cent.)—exceedingly soluble.

Metaphosphoric acid-insoluble; boiling no effect.

Orthophosphoric acid—very soluble, forming an absolutely clear solution; boiling has no decided effect.

Sodic metaphosphate-insoluble; boiling no effect.

Sodic orthophosphate—soluble in a much larger amount than is necessary in dissolving the water-venom-globulin; boiling has no effect, unless to clear the solution some.

Potassic sulphate-insoluble; boiling no effect.

Calcic chloride—less soluble than water-venom-globulin.

Acetic acid (5 per cent.)—very soluble.

Acetic acid (glacial)-very soluble.

The Dialysis-venom-globulin.—The filtrate, after the separation of the water-venom-globulin and copper-venom-globulin, still gives a decided amount of coagula by boiling, and also all of the characteristic color reactions for proteids. If the filtrate be now subjected to dialysis, best by means of a large dialyser placed over running water, in the course of twenty-four hours a considerable amount of precipitate will be deposited within the dialyser, and which may be collected on a filter, and repeatedly washed as in the preparation of the preceding globulins.

If dialysis is carried on for a sufficient length of time the whole of this principle will be precipitated, since the filtrate from the globulin will give no coagula by boiling, nor any precipitate by strong nitric acid. A proteid still remains in solution, however, which has been already alluded to as being a peptone. This body being less dialysable than the salts which hold the globulins in solution, still remains in part within the dialyser, even when the salts are so fully withdrawn as to entirely precipitate the globulins.

The dialysis-venom-globulin gives the following reactions:—

Decided reactions with the usual proteid tests.

Sodic chloride (0.75 per cent.)—insoluble.

(10 " )—slightly soluble.

(crystals)—more soluble, forming a very cloudy solution; boiling clears the solution some; the same degree of clearing does not occur in the mixture without the sodic chloride.

—the addition of carbonic acid to the solution with crystals causes a beautiful clear solution, which is made cloudy by boiling.

Carbonic acid-soluble; cloudiness by boiling.

Sodic carbonate-very soluble; boiling no effect.

Hydrochloric acid (0.4 per cent.)-very soluble.

Metaphosphoric acid—rendered of a yellowish tint; not appreciably dissolved; boiling no appreciable effect.

Orthophosphoric acid-very soluble; boiling no effect.

Sodic metaphosphate-very soluble, forming a very clear solution; boiling no effect.

Sodic orthophosphate—slightly soluble; dissolving slowly in excess, forming a slightly turbid solution; boiling clears absolutely.

Potassic sulphate-insoluble; boiling no decided effect.

Calcic chloride—soluble by the addition of a comparatively larger amount; boiling causes coagulation.

Acetic acid (5 per cent.)—very soluble. Acetic acid (glacial)—very soluble.

The Venom Peptone.—After the separation of the dialysis-globulin the filtrate, as before stated, gives no coagula by brief boiling, but by testing with the usual proteid tests very decided reactions are obtained. It is further found that if the above filtrate is placed in a fresh dialyser, that the principle giving the proteid reactions will readily pass through the membrane. The fact that this substance will dialyse readily, and that it is not immediately coagulated at the temperature of boiling water, and not precipitated by cupric sulphate and ferric chloride, nor by neutralization, renders it certain that it belongs to a peculiar class of bodies which are known as peptones, and which are ordinarily the result of peptic or tryptic digestion. This peptone may also be prepared by briefly boiling the solution of venom, which coagulates the other albuminous principles, and leaves this in solution; but the coagula caused by boiling the solution of Crotalus are so extremely fine, that it is impossible to filter the mixture clear, even by repeated filtration through many thicknesses (7) of the best filter paper; furthermore, continued boiling causes a breaking down of the peptone with the apparent formation of fine coagula (see Cobra peptone, p. 17). We, however, prepared the peptone by dialysis, and obtained the following reactions:-

No immediate coagulation at a temperature of 100° C.

Full reactions with the proteid color tests.

No precipitate with weak or strong nitric acid.

Ferric chloride-no precipitate.

Cupric sulphate-no precipitate.

Mercuric chloride-decided precipitate.

Absolute alcohol-precipitate; precipitate redissolved by the addition of water.

Mercuric nitrate-decided precipitate.

Potassic hydrate—precipitate by saturation; precipitate redissolved by the addition of nitric acid, forming a decidedly yellowish solution, which becomes decolorized by further addition of acid.

Potassic ferrocyanide in presence of weak acetic acid-a precipitate.

To revert now to the globulins and their distinctive features, it seems clear that these principles must exist in the venom as distinct bodies, and are not simply representatives of a single globulin which have arisen through our manipulations. The first distinguishing feature between them is represented in the process of isolation, but if we place the reactions of the different globulins in parallel columns,

we find that, while they have very close resemblances, as they naturally should since they are so intimately related, they are very readily distinguished from each other. The properties of all globulins are so readily affected by even the simplest manipulations that it is likely that mere precipitation may affect them in regard to their solubility, while drying may completely destroy this property. Having these facts in mind, it seems almost a necessity that the processes through which we put these globulins, in order to get them isolated in a pure state, has more or less modified their chemical, and possibly their physiological properties.

The tests made with these globulins were all made at different times, the one globulin was examined one day, and another on another day, so that the reactions given are not absolutely accurate as a matter of comparison, but only relative, since the standard of solubility, which was of course an arbitrary one, was simply carried in the mind throughout the examinations. We believe, however, that they are practically correct.

Reagent. ·	Water-venom-globulin.	Copper-venom-globulin.	Dialysis-venom-globulin.
Sodic chloride (10 p. c.) Carbonic acid	Soluble Soluble	Insoluble Insoluble	Slightly soluble.
Sodic carbonate	(Very soluble; not precipitated by CO.	Very soluble; pre-)	Very soluble.
Hydrochloric acid (0.4 p. c.)	Very soluble	Very soluble	Very soluble.
Metaphosphoric acid	Insoluble	Insoluble	(Insoluble; rendered
Orthophosphoric acid	Soluble	Very soluble	Very soluble.
Sodic metaphosphate	Insoluble	Insoluble	Very soluble.
Sodic orthophosphate	Very soluble	Less soluble	Still less soluble.
Potassic sulphate	Very soluble	Insoluble	Insoluble.
Calcic chloride	Very soluble	Less soluble	Less soluble.
Acetic acid (5 per cent.)	Very soluble	Soluble	Very soluble.
Acetic acid (glacial)	Very soluble	Soluble	Very soluble.

The venom of the Moccasin (*Ancistrodon piscivorus*) was subjected to an analysis similar to that of the Crotalus, the isolated proteids giving the following reactions:—

Water-venom-globulin.

Decided reactions with the usual proteid color tests.

Boiling—clears the mixture without the apparent formation of any coagula. Sodic chloride (0.75 per cent.)—insoluble.

(10 ")—somewhat soluble, solution not absolutely clear; boiling clears absolutely without the formation of coagula.

(crystals)—somewhat soluble; solution not precipitated by carbonic acid.

Carbonic acid-insoluble.

Sodic carbonate—soluble, forming slightly turbid solution; boiling clears the solution without giving coagula; the addition of crystals of sodic chloride to the hot boiled solution causes m precipitate, this precipitate being coagulated by boiling.

Hydrochloric acid (0.4 per cent.)—somewhat soluble.

(5 " )—soluble.

Metaphosphoric acid-insoluble.

Orthophosphoric acid-soluble.

Sodic metaphosphate-slightly soluble; solution rendered clearer by boiling.

Sodic orthophosphate—soluble; solution rendered absolutely clear by boiling.

Potassic sulphate-soluble; solution rendered absolutely clear by boiling.

Calcic chloride-soluble; solution rendered clearer by boiling.

Acetic acid (5 per cent.)-insoluble.

Acetic acid (glacial)—insoluble?

### Copper-venom-globulin.

Boiling-clears somewhat; no coagula.

Sodic chloride (0.75 per cent.)-insoluble.

(10 ")-insoluble.

(crystals)—insoluble; boiling partially clears without the formation of any coagula.

Carbonic acid-somewhat soluble; boiling clears absolutely.

Sodic carbonate-very soluble; boiling no effect.

Hydrochloric acid (0.4 per cent.)—very soluble.

Metaphosphoric acid-insoluble; boiling appears to clear slightly.

Orthophosphoric acid-very soluble.

Sodic metaphosphate-insoluble; boiling clears somewhat.

Sodic orthophosphate-somewhat soluble; boiling clears beautifully.

Potassic sulphate-insoluble; boiling clears slightly.

Calcic chloride—slowly dissolved; not so soluble as water-globulin; boiling gives a slight cloudiness.

Acetic acid (5 per cent.)—soluble.

Acetic acid (glacial)—soluble.

### Dialysis-venom-globulin.

Boiling—clears almost absolutely without the apparent formation of coagula; boiled solution precipitated by saturation with crystals of sodic chloride.

Sodic chloride (0.75 per cent.)-insoluble.

(10 ")—somewhat soluble; dissolves slowly, forming a slightly turbid solution; boiling seems to clear some without the formation of coagula.

Carbonic acid-very soluble; slight turbidity by boiling.

Sodic carbonate-very soluble; boiling no effect.

Hydrochloric acid (0.4 per cent.)-very soluble.

Metaphosphoric acid-slightly soluble; yellowish tint; boiling clears slightly with the formation of coagula.

Orthophosphoric acid-very soluble; boiling no effect.

Sodic metaphosphate—insoluble.

Sodic orthophosphate-soluble; boiling no effect.

Potassic sulphate—somewhat soluble.

Calcie chloride—very soluble, form a beautiful clear solution; boiling causes slight turbidity.

Acetic acid (5 per cent.)—soluble

Acetic acid (glacial)-soluble

#### Moccasin Peptone.

- 1. Readily dialysable.
- 2. Not immediately coagulated at a temperature of  $100^\circ$  C., but gradually coagulated by prolonged boiling (see Cobra peptone, p. 17).
  - 3. Reaction with the xantho-proteic test (nitric acid and ammonia)
  - 4. Reaction with Millon's reagent (mercuric nitrate)
  - 5. No precipitate with weak or strong nitric acid.
  - 6. No precipitate with CO2.
  - 7. No precipitate with ferric chloride.
  - 8. No precipitate with cupric sulphate.

- 9. Precipitated by mercuric chloride.
- 10. Precipitated by absolute alcohol.
- 11. Gives a faint reddish tinge with a strong solution of potassium hydrate, and a trace of cupric sulphate.
  - 12. Not precipitated by strong acetic acid (glacial).
  - 13. Precipitated by very dilute acetic acid; precipitate being redissolved by further addition of acid.
  - 14 Full reaction with Adamkiewicz's test for proteids.
- 15. Precipitated by adding a large quantity of sodium chloride, the precipitate being redissolved on the addition of a large quantity of glacial acetic acid.
  - 16. Precipitated by mercuric nitrate.
- 17. Precipitated by absolute alcohol; precipitate being apparently redissolved on the addition of vater.

18. Precipitated by saturation with potassium hydrate; precipitate being redissolved by the addition of nitric acid, with the formation of a decidedly yellow solution (xantho-proteic) which becomes decolorized by addition of acid.

19. Precipitated by potassium ferrocyanide in the presence of weak acetic acid.

Venom-peptone by dialysis gives identical reactions.

For convenience of comparison we append here in parallel columns the principal reactions of the Moccasin globulins, remembering in this connection the difference in the properties manifest in their methods of preparation.

Reagent.	Water-venom-globulin.	Copper-venom-globulin.	Dialysis-venom-globulin.
Boiling	Clears almost abso-	Clears some	Clears some.
Sodic chloride (10 per cent.)	Lutely   Somewhat soluble	Insoluble	Somewhat soluble.
Carbonic acid	Insoluble	Somewhat soluble	Very soluble,
Sodic carbonate	Soluble	Very soluble	Very soluble.
Hydrochloric acid (0.4 p. c.)	Somewhat soluble	Very soluble	Very soluble.
Metaphosphoric acid	Insoluble	Insoluble	Slightly soluble.
Orthophosphoric acid	Soluble	Very soluble	Very soluble.
Sodic metaphosphate	Somewhat soluble	Insoluble	Insoluble.
Sodic orthophosphate	Soluble	Less soluble	Soluble.
Potassic sulphate	Soluble	Insoluble	Slightly soluble
Calcic chloride	Soluble	Insoluble	Very soluble.
Acetic acid (5 per cent.)	Insoluble	Soluble	Soluble.
Acetic acid (strong)	Insoluble	Soluble	Soluble.

For reactions of the peptones of the various venoms see p. 19.

Cobra Venom.—We have been able to isolate in Cobra venom only two proteids, and these correspond in their characters to the two types of proteids found in the venoms of the Crotalus and Ancistrodon. In other words, we have isolated a globulin and a peptone-like principle. The globulin we are able to precipitate completely by the addition of a proper amount of distilled water, after which the solution gives no coagulum by boiling. There is then left in solution a proteid, which evidently belongs to the peptones, although giving some extraordinary reactions.

The venom-globulin thus isolated and purified, as in the preparation of the globulins previously mentioned, possesses the peculiar properties of the globulin family, and, in accordance with our nomenclature, since it is entirely precipitated by the addition of distilled water, is a *water-venom-globulin*.

The following are some of the reactions given by this substance (the water-venom-globulin suspended in distilled water):—

Boiling-coagulates.

Sodic chloride (0.75 per cent.)—insoluble.

(10 ")—soluble; boiling gives slight turbidity.

-sodic chloride solution apparently unaffected by carbonic acid.

Carbonic acid-insoluble.

Sodic carbonate-soluble, slightly turbid solution; boiling makes perfectly clear.

Hydrochloric acid (0.4 per cent.)-soluble.

Metaphosphoric acid-insoluble; boiling no appreciable effect.

Orthophosphoric acid-very soluble; boiling makes solution absolutely clear.

Sodic metaphosphate-insoluble; boiling no appreciable effect.

Sodic orthophosphate-somewhat soluble; boiling renders perfectly clear.

Potassic sulphate—somewhat soluble.

Calcic chloride-soluble; opalescence of solution increased by boiling.

Acetic acid (5 per cent.)-soluble.

Acetic acid (glacial)-soluble.

Cobra-venom-peptone.—The venom-peptone from Cobra may be prepared by boiling, thus coagulating the globulin, or by dialysis. Great difficulty is experienced in the former process, since the coagula are so fine that it is impossible, save in rare instances, to obtain a clear filtrate, and as to these we have no explanation to offer for the exception. The peptone prepared by boiling or by dialysis gives identical reactions.

Before detailing the reactions of this body it may be well to notice a peculiar property exhibited by all venom-peptones which gives them a very distinguishing feature. After boiling the venom for a few minutes and then filtering, the filtrate will again give further coagula by continued boiling, and so the process of boiling and filtering, and reboiling the filtrate may go on repeatedly, yet the clear filtrate will in every instance give fresh coagula. Indeed the boiling process may be continued for an hour or more, and yet at the end of that time the filtrate will still yield coagula. However, after the venom solution has once been boiled, coagulation does not recommence in the filtrate until it has been boiled for a few moments. These most interesting facts suggest that the coagula formed after the first boiling are due to a gradual decomposition of what is in some sense a non-coagulable proteid, since coagulable proteids all coagulate at once and completely when a definite temperature is reached; the coagula which follow repeated or prolonged boiling appear to be due to such a decomposition of proteids as violent chemical or physical action could alone account for.

It seems to us perfectly clear that the body which is thus gradually broken up by prolonged boiling is a *peptone*. Our principal reasons for this belief are that the body so coagulated is very readily dialysable, is not precipitated by ferric chloride, or cupric sulphate, and in the case of the Cobra is not precipitated by absolute alcohol, or *mercuric chloride*, is not coagulated below the boiling point, and in fact not until boiling has gone on for a few moments. The following reactions seem to be sufficiently characteristic.

These results we obtained from a solution of the Cobra-venom-peptone obtained 3 April, 1886.

by dialysing venom for forty-eight hours. The dialysate was perfectly clear and neutral in reaction:—

Boiling—no result until after a few moments, when it becomes cloudy, the cloudiness increasing as boiling continues; strong nitric acid dissolves the precipitate.

Color reactions for proteids—the xantho-proteic, Millon and Biuret reactions are all obtained.

Ferric chloride—no effect.

Cupric sulphate-no effect.

Mercuric chloride—no effect.

Mercuric nitrate-decided precipitate.

Absolute alcohol-no precipitate.

Potassic ferrocyanide + weak acetic acid-precipitate.

Nitric acid (strong)-no precipitate.

Hydrochloric acid (strong)-no precipitate.

Acetic acid (strong)-no precipitate.

Sodic chloride (saturation)—precipitate; acetic acid, large quantity, dissolves.

Potassic hydrate to saturation-precipitate.

Tannic acid-decided precipitate.

Basic acetate of lead-decided precipitate.

Several very remarkable facts are the coagulation by prolonged boiling and the non-precipitation by mercuric chloride and absolute alcohol. Since this peptone is precipitated by weak acetic acid in the presence of potassic ferrocyanide it has a slight resemblance to Meissner's A peptone, although materially differing, as some of the above reactions show, from any other described body of this class.

As a matter of some interest, it is desirable to know if similar globulins in different venoms are identical in their chemical nature, or whether they give any reactions which may distinguish them. We have accordingly, as in previous cases, placed the reactions of the corresponding globulins side by side.

### I. Water-venom-globulin.

Reagent.	Crotalus horridus.	Ancistrodon piscivoris.	Cobra.
Boiling	Coagulates	Apparently dissolves	Coagulates.
Sodic chloride (10 per cent.)	Soluble	Somewhat soluble	Soluble.
Carbonic acid	Soluble	Insoluble	Insoluble.
Sodic carbonate	Soluble	Soluble .	Soluble.
Hydrochloric acid (0.4 p. c.)	Soluble	Somewhat soluble	Soluble.
Metaphosphoric acid	Insoluble	Insoluble	Insoluble.
Orthophosphoric acid	Soluble	Soluble	Soluble.
Sodic metaphosphate	Insoluble	Somewhat soluble	Insoluble.
Sodic orthophosphate	Very soluble	Soluble	Somewhat soluble.
Potassic sulphate	Very soluble	Soluble	Somewhat soluble.
Calcic chloride	Very soluble	Soluble	Soluble,
Acetic acid (5 per cent.)	Soluble	Insoluble	Soluble.
Acetic acid (strong)	Soluble	Insoluble	Soluble.

# II. Copper-venom-globulin.

Reagent.
Boiling Sodic chloride (10 per cent.) Carbonic acid Sodic carbonate Hydrochloric acid (0.4 p. c.) Metaphosphoric acid Orthophosphoric acid Sodic metaphosphate Sodic orthophosphate Potassic sulphate Calcic chloride Acetic acid (5 per cent.) Acetic acid (glacial)

## III. Dialysis-venom-globulin.

Reagent.
Boiling Sodic chloride (10 per cent.) Carbonic acid Sodic carbonate Hydrochloric acid (0.4 p. c.) Metophosphoric acid Orthophosphoric acid Sodic metaphosphate Sodic orthophosphate Potassic sulphate Calcic chloride Acetic acid (5 per cent.) Acetic acid (glacial)

It will be noticed by a careful comparison that the corresponding principles in different venoms differ quite as much from each other as the globulins in any one variety of venom.

Venom Peptones.—We have not been able to detect any chemical differences in the venom peptones of the Crotalus and Ancistrodon. Cobra venom peptone is distinguished from that of the Crotalus and Ancistrodon by its non-precipitability by mercuric chloride and absolute alcohol.

Daboia Venom.—We have had a small quantity (a few grains) of Daboia venom at our disposal, but too little to attempt any detailed chemical investigations. In two examinations, however, with very small quantities, we separated two bodies corresponding to those in Cobra, that is a water-venom-globulin and a peptone. The former exists in exceedingly small quantity while the latter dialyses with apparently much more difficulty than that of the Cobra.

The Proportions of Proteid Constituents in Different Venoms.—An examination of good specimens of the dried venoms of the Crotalus adamanteus, Ancistrodon piscivorus, and Cobra gives us the following proportions of the globulins and peptones:—

```
Crotalus adamanteus—
          0.5 gram dried venom = water-venom-globulin
                                                         0.0495
                                  copper-venom-globulin 0.0375
                                  dialysis-venom-globulin 0.0360
                                                         0.1230 = globulins.
                                                         0.3770 = peptone1 (estimated.)
Ancistrodon piscivorus—
       0.3364 gram dried venom = water-venom-globulin
                                                         0.0034
                                   copper-venom-globulin
                                                         0.0182
                                   dialysis-venom-globuliu 0.0047
                                                         0.0263 = globulins.
                                                          0.3101 = peptone1 (estimated).
   According to this estimate there would be in 0.5 gram 0.0391 globulins.
                                                     0.4609 peptone.1
Cobra-
           0.2 gram dried venom = water-venom-globulin 0.0035
                                                 peptone1 0.1965 (estimated).
   According to this estimate there would be in 0.5 gram 0.0087 globulin.
                                                        0 4912 peptone.1
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From these analyses it will be observed that the dried venom of the *Crotalus adamanteus* contains 24.6 per cent. of globulins, the Ancistrodon 7.8 per cent., and the Cobra 1.75 per cent. The globulins in the Crotalus venom appear to be in almost equal proportions, while in the Ancistrodon the copper-venom-globulin is about five times greater than the water-venom-globulin and about four times more than the dialysis-venom-globulin—the two latter being nearly in the same proportion—therefore constituting more than half of the entire weight of globulins.

These differences in the proportions of the various globulins in any specimen of venom and the differences in the proportions of globulins and peptones in different venoms are of immense importance in affording an explanation of the physiological peculiarities exhibited in poisoning by different species of snakes. It will be observed that the proportion of globulins in Crotalus is over three times the quantity in the Ancistrodon, and nearly fifteen times that in the Cobra.

<sup>&</sup>lt;sup>1</sup> Including the salts, which are in very small quantity.

#### CHAPTER III.

#### EFFECTS OF VARIOUS AGENTS ON VENOM..

Effects of Various Agents on Venom.—The influence of acids, alkalies, and salts on venoms has been studied by several observers, with results which vary remarkably; so that for this and for other reasons there is still room for research of this nature. The questions thus brought up have a twofold interest, the one chemical and the other toxic. Numerous bodies precipitate or dissolve venoms; but among those which most plainly alter these poisons, only a few so change them as to lessen or destroy their poisonous efficiency. Unfortunately, that which alters the poison as such, is always equally destructive to the tissues of the body, and no agent as yet employed can be shown to have the power to enter the blood, and there affect the venom without doing harm to other albuminous substances. So far, we have learned only that amidst the agents which precipitate venom, there are some which weaken or annihilate its toxic force. They can be thrown into the fang tracks, and where they are made to mingle with the venom will destroy it as impartially as they do the innocent tissues in which it lies.

It may not be out of place to remark that we have made no direct study of agents as antidotes. Too much yet remains to be known of these poisons before we can hope to find a means of antagonizing them physiologically. Our local or chemical antidotes are sufficiently effective.

Effect of Desiccation of Venom.—Allowed to dry at ordinary temperatures, the venoms retain their poisonous activity almost unaltered. When again water is added they act as usual, except that, owing perhaps to imperfections in redissolution, they do not produce as much local effect within as short a time as do the fresh fluid venoms. Neither, it may be added, is the general toxic influence quite as rapid when venom has been once desiccated.

The Effects of Various Agents on the Toxicity of Venoms. Age.—Some fresh venom of the Orotalus horridus was dissolved in an equal quantity of pure glycerine and the vial corked and sealed in 1863. In November, 1882, the contents of the vial were examined. The solution was perfectly clear, and had at the bottom a small mass of what appeared to be a fungous growth. Some of the venom was now injected into various animals to test its toxicity. The following experiment attests its power:—

Experiment.—Pigeon. Injected, at 5:12 P. M., into the muscles of the thigh about six drops of the above glycerin solution.

5:14. Animal decidedly weakened.

5:25. There is considerable blackening of the tissues about the point of injection, the parts

being much swollen, the leg stiff, the muscles at the point of injection are paralyzed, and sensibility of the leg destroyed. The pigeon lies on its side unable to stand, is exceedingly prostrated, and breathes laboriously. Observation now ceased until 8 A. M. following morning, when the animal was found dead and in general rigor mortis, excepting the muscles at point of injection.

Autopsy.—The tissues were dark, congested, and suffused with serum for an area of one and a half inches from point of injection. The viscera of the thoracic and abdominal cavities appeared slightly congested; the heart was arrested in systole and contained dark clots; the blood everywhere was dark and clotted. Microscopically the muscular fibres did not appear to be greatly disorganized, although in some of the fibres no transverse striæ or nuclei could be discovered.

The Effects of Dry Heat. Experiment.—0.03 gram of dried (Crotalus adamanteus) venom was subjected in a dry oven to a gradually rising temperature to 83.5° C., and maintained at this point for half an hour. The venom, after cooling, was dissolved in 1 c. c. of distilled water.

- 2:57. Injected the above into the thigh of a pigeon.
- 4:49. Violent convulsions and death. Local effects decidedly marked.

Experiment.—Repeated the above, but subjecting the venom to a temperature of 100 C. for ten minutes.

- 3:42. Injected into the thigh of a pigeon.
- 6:00. No decided symptoms. On the following morning the animal was dead. The local effects were marked.

Experiment.—Repeated the above, but subjecting the venom to a temperature of  $110^{\circ}$  C. for thirty minutes.

- 4:46. Injected into the thigh of a pigeon.
- 5:25. Convulsions.
- 5:45. Died. The local effects were marked.

From these results it seems clear that heating the dry venom to a degree above boiling point does not apparently alter its poisonous activity. The delay in the occurrence of death in the second experiment suggests that the venom was altered, but in the third experiment in which the temperature was even higher, and this degree of heat maintained for a much longer time, death occurred even sooner than in the first experiment, showing that the differences must have been dependent upon conditions in the animals.

The Effects of Moist Heat. Experiment.—0.03 gram dried venom (Crotalus adamanteus) was dissolved in 1 c. c. distilled water, and gradually heated until a flocculent precipitate occurred.

This was injected into the thigh of a pigeon in the evening. The next morning the animal was found dead.

Experiment.—0.03 gram dried venom (Crotalus adamanteus) was dissolved in 1 c. c. distilled water and subjected to a gradually rising temperature to 50° C.

- 3:49. Injected the above into the breast muscles of a pigeon.
- 3:51. Very weak, pupils apparently contracted, trembling; breathing laborious.
- 4:00. Dead. At the point of injection the tissues were decidedly congested and purplish and suffused with blood. The blood generally was fluid, but some soft clots were found in the abdominal vessels.

Experiment.—Subjected a similar amount of venom in solution to a rising temperature to  $65^{\circ}$  C.

4:01. Injected into the breast muscles of a pigeon.

4:05. Head depressed.

4:10. Very weak, falls on the side.

5:02. Dead. The local effect is not so marked as in the previous experiment. The injection was merely subcutaneous. The viscera did not appear congested or abnormal; the heart was arrested in systole; blood everywhere fluid and dark; no ecchymoses in the peritoneum; muscles appear darker than normal.

Experiment.—Repeated the above, but increasing temperature to 74° C.

4:13. Injected into the breast muscles of a pigeon.

4:19. Weak, falls on side.

5:05. Dead. Blood clotted; local effect the same as in previous experiment.

Experiment.—Results the same as in the last experiment, excepting that the local effects were more marked. This animal lived a half hour longer than the last, which will probably account for the difference.

Experiment.—The same, but subjecting the solution to 76.5° C.

4:04. Injected into the breast muscles of a pigeon.

4:27. Unable to stand.

6:00. Nearly dead.

Following morning. Extremely feeble, too weak to stand; there is a muco-sanguinolent discharge from the bowels.

Second day. Very feeble.

Third day. Recovering.

Experiment.—The same, but subjecting the solution to 79.5° C.

4:00. Injected into the breast muscles of a pigeon.

5:50. No symptoms.

Following morning animal well.

Experiment.—The same, but subjecting the solution to 81° C.

4:31. Injected into the breast muscles of a pigeon.

4:45. Apparently a little stupid.

5:50. No further effect.

Following morning. Animal well.

Second morning. Animal well.

Experiment.—Boiled a similar amount of solution for two minutes.

3:26. Injected into the breast muscles of a pigeon.

4:30. No effect.

Following morning. No effect.

The above very interesting series of experiments clearly shows that the effect of heat on a solution of venom is very positive, that the toxicity of venom is decidedly affected, and that the greater the increase of temperature between certain limits the greater is the destruction of the poisonous power of the venom. It will be observed in the second experiment, which is the first in which any positive temperature was observed, that the animal died in about ten minutes after injection; in the third experiment in about one hour; in the fourth and fifth experiments in about three-fourths of an hour, and an hour and three-quarters respectively; in the sixth experiment in about two hours; the animal was nearly

dead, but finally recovered in the seventh experiment and in the subsequent ones there were no poisonous symptoms. It will thus be observed that there is a gradual impairment of the toxicity of the venom increasing with the increase of temperature, and that when we reach 76.5° C. we have almost reached the temperature at which toxicity seems to be completely destroyed. We say seems completely destroyed, because we have found that the solution is still toxic even when boiled, although there is not sufficient active poisonous matter left after boiling in the small amount of venom we used in this group of observations to cause decidedly poisonous effects in pigeons.

The results of boiling solutions of *Moccasin* and *Cobra* venoms are quite different from the above, as the following experiments clearly show:—

Experiment.—Dissolved 0.015 gram dried Moccasin in 1 c. c. distilled water, and gradually heated to 78° C.

3:40. Injected into the breast of a pigeon.

3:50. Rocking.

4:45. Nearly gone; some local effect.

Following morning the animal was dead. The local effect (darkening) was marked, but not comparable to that caused by the unboiled venom.

Experiment.—Boiled 0.015 gram dried Moccasin (piscivoris) dissolved in 1 c. c. distilled water for one minute.

3:28. Injected the above into the breast muscles of a pigeon.

3:35. Too weak to stand.

4:15. Dead. There are no local effects.

Experiment.—Dissolved about  $1\frac{1}{2}$  minims of fresh Moccasin venom in about 1 c. c. distilled water, then boiled in a test-tube, filtered and injected one-half into the breast muscles of a pigeon at 4:30.

4:55. Very slight local effect; darkening and swelling; the animal is weak and has respiratory disturbance.

Injected the other half.

5:00. Rocking; irregular breathing; somewhat stupefied.

5:20. Eyes closed; stupefied; breathing irregular.

Following morning. There was a large, light-colored, edematous swelling (see Plate No. 1) within, which was a cavity about an inch in diameter, full of broken-down tissue, having a grayish muddy, gangrenous appearance, and a putrefactive odor, while the surrounding muscular tissues were normal in appearance.

It will be observed in this series of experiments with the Moccasin venom that there is also a very decided alteration in the poisonous properties of the venom. But here we find that although the amount of venom used was only one-half the quantity employed in the Crotalus series, boiling does not destroy its ability to kill. It will also be noticed here, as in the case of the Crotalus, that a sufficient degree of heat has an obvious effect on the power of the venom to produce the peculiar lesions at the point of injection.

The effect of heat upon solutions of Cobra venom is not so marked.

Experiment.—0.03 gram dried Cobra venom was dissolved in 1 c. c. distilled water and subjected to a temperature gradually rising to 74° C.

4:10. Injected into the breast muscles of a pigeon.

4:16. Unable to stand.

4:20. Dead.

Experiment.—The same, excepting that the temperature was raised to 79.5° C.

4:12. Injected as above.

4:21. Unable to stand.

4:25. Dead.

Experiment.—The same, solution being brought to boiling point in a test-tube.

4:45. Injected into the breast muscles of a pigeon.

5:00. Unable to stand.

5:03. Convulsions followed by death.

Experiment.—0.015 gram dried venom dissolved in 1 c. c. distilled water and boiled in a test-tube for about two minutes.

3:51. Injected into the breast muscles of a pigeon.

4:15. Unable to stand.

4:22. Dead. No local effects.

From these experiments it appears that the toxicity of venom is not impaired by brief heating as high as 79.5° C., the time of death being in these experiments about the same as with the unheated solution. In the last two experiments in which the solution was boiled, the time of death is delayed, especially so in the last experiment, but here it must be observed that but one-half the dose was used.

In one experiment made on the venom of the Copperhead (Ancistrodon contortrix) the effect seemed to be in degree between that of the Crot us and Ancistrodon piscivorus.

Experiment.—0.03 gram dried venom was dissolved in 1 c. c. distilled water and boiled in a test-tube for two minutes.

5:00. Injected into the breast muscles of a pigeon.

5:10. Unable to stand.

5:20. Incoördination.

6:00. Very weak.

Following morning. Dead. There were very slight local effects; the blood was clotted in soft black clots; heart arrested in systole, auricles full of clots. The interior of the thoracic cavity had a mucky brownish appearance; the viscera did not appear congested, and there were no ecchymoses.

A similar dose of the unheated copperhead venom kills promptly with decided local effects. It will thus be apparent that boiling decidedly alters its toxic power.

The effect of boiling on the venom of the Crotalophorus is as decided as on that of the Crotalus.

Experiment.—Two drops of the fresh venom of the Crotalophorus was dissolved in 1 c, c, distilled water and boiled for a moment.

4:58. Injected into the breast muscles of a pigeon.

6:15. In good condition; no symptoms up to this time, excepting a little tendency to droop.

Following evening. Animal normal.

The venom of the Coral snake (Elaps fulvius) is affected to a less degree.

<sup>&</sup>lt;sup>1</sup> Very prolonged boiling, as has been shown by Fayrer and by Ward, lessens greatly, and at last destroys toxicity in cobra venom. The efficient cobra peptone is, as we have seen, converted into a coagulable albuminoid, which is then incapable of destroying life.

<sup>4</sup> April, 1886.

Experiment.—Boiled 0.015 gram dried Coral venom dissolved in 1 c. c. distilled water.

Time of injection?

5:45. Very weak.

6:00. Nearly dead.

6:10. Dead. No local effects. Blood coagulates perfectly.

A smaller amount of venom unboiled kills in from 10-15 minutes with decided local effects.

From the experiments with the venom of the *Crotalus adamanteus* detailed above it appears as though the toxicity of the venom was completely destroyed by boiling, but Weir Mitchell found some years ago that boiling did not destroy the poisonousness of the venom of the *Crotalus durissus*, and further work of our own led us to believe that the want of toxicity of our boiled solutions was only apparent, and that there was accordingly a poisonous principle still present, but not in deadly quantities. We therefore made some further observations, using larger amounts of venom.

Experiment.—Dissolved three drops of fresh Crotalus adamanteus venom in 1.5 c. c. distilled water and boiled.

4:40. Injected into the breast muscles of a pigeon.

6:10. No positive effects.

Following morning. Dead, no characteristic local effects.

Experiment.—Dissolved 0.12 gram venom (Crotalus adamanteus) in 2 c. c. distilled water and boiled for two or three minutes.

4:40. Injected the above into two pigeons, giving each half.

Death within fourteen hours in both pigeons. There was some slight local effect, but nothing comparable to what is observed in the unheated venom. There were no extravasations, and the blood was clotted. The stench from putrefaction at the points of injection was very great, and the muscles around them presented a pale-grayish color as though they had been boiled.

A like result was obtained in the case of another pigeon experimented on in the same way.

From the above series of experiments it is perfectly clear that heating the dissolved venom beyond a definite point, varying no doubt in different venoms, lessens its toxic power. Boiling for some minutes does not destroy the poisonous capacity of the venoms, but simply impairs this quality to a varying degree, depending upon peculiarities in the toxic constituents, as we shall hereafter have reason to observe.

Fayrer and Wall, as already noted, found that *prolonged* boiling of solutions of Cobra venom completely destroyed the poisonous activity of that secretion. We accordingly made some similar experiments with solutions of the venom of the *Crotalus adamanteus* with analogous results.

Experiment.—0.03 gram of the dried venom of the Crotalus adamanteus was dissolved in a little distilled water and boiled for ten minutes in a water bath After being allowed to cool it was injected into the breast of a pigeon.

1:56. Injection practised.

1:57. Weak.

2:00. Convulsions.

2:37. Since last observation has been lying on its side, very weak.

2:43. Dead.

In a subsequent experiment the solution of venom was boiled for forty minutes. Three minutes after the injection the pigeon vomited; no other toxic symptoms were observed. In another experiment, in which the venom was boiled for one hour, no symptoms occurred but vomiting. Both of these pigeons were watched for three days, but in neither of them did any poisonous symptoms ensue.

The Effects of Alcohol.—When alcohol is added to fresh venom or to an aqueous solution of venom a copious white precipitate occurs. The following experiments were made to determine if the active principles were entirely precipitated by the alcohol, and if the precipitate was poisonous.

Experiment.—Four drops of the venom of the Crotalus adamanteus were placed in 1 c. c. absolute alcohol. The precipitate was filtered and washed with an additional amount of alcohol, the filtrate then being evaporated spontaneously to 1 c. c.

The *precipitate* was placed in 1 c. c. distilled water and injected into the breast muscles of a pigeon at 5:11.

5:17. Too weak to stand.

5:21. Dead. There was very little local effect.

The *filtrate* was injected into another pigeon, as above, at 5:22.

5:26. Vomits; no further effects.

From this experiment it is obvious that the presence of alcohol does not destroy toxicity. Further observations were made to learn the effect of a more prolonged action, and if the precipitate was soluble in water.

Experiment.—0.06 gram of dried Crotalus adamanteus was dissolved in 3 minims of distilled water and this was added to 3 c. c. absolute alcohol (Squbb's) causing a dense precipitate. The mixture was allowed to stand for three days. It was then filtered, the precipitate being several times washed with the filtrate and finally with fresh absolute alcohol.

The precipitate was finally washed from the filter by distilled water, allowed to dry, then digested in distilled water for twenty-four hours, and, after being filtered, was washed with distilled water. The filtrate was cloudy, and on being allowed to stand for one and a half hours cleared somewhat, there being an upper layer of clear fluid and some sediment.

One-fourth of the filtrate was now injected into the breast muscles of a pigeon at 4.43.

4:54. Unable to stand.

5:10. Dead. There is exceedingly little local effect. The tissues at point of injection are suffused with blood.

5:45. Blood still fluid.

To one-fourth of the filtrate one minum of acetic acid was added, which caused the mixture to become clear.

4:41. Injected into a pigeon as above.

4:52. Rocking.

4:54. Down.

5:58. Dead. There is absolutely no local effect and there is no suffusion of blood in the tissues as in the previous experiment.

To one-fourth of the filtrate a few crystals of sodic chloride were added, which rendered the solution clear.

4:49. Injected as before.

4:55. Rocking.

4:58. Down.

5:57. Dead. The local effect is intense; great blackening and infiltration of fluid blood.

It will have been seen that even after subjection for three days to the action of absolute alcohol the venom has not lost its toxicity. It further appears that the addition of acetic acid or sodic chloride, while rendering the undissolved material soluble delays the time of death, and that the local effects of the poison are destroyed by the acid and intensified by the sodic chloride. The action of the acid is probably due either to a powerful local constricting action on the tissues or else to a modification of the properties of the poison. We can give no reason for the cause in the delay of death after the addition of the sodic chloride. As the animal in this observation lived longer than in the first, the increased local effect may be in this way partially accounted for.

The filtrate becomes very turbid by boiling, and gives a decided precipitate with nitric acid, thus proving that the water has actually dissolved some of the precipitate, and consequently that the toxicity of the filtrate cannot depend merely upon the undissolved particles of precipitate carried through the filter.

It is interesting to learn whether alcohol dissolves any poisonous element of the venom. In one of the above experiments the only effect following the injection of the alcohol filtrate was vomiting, but the objection may be made that the alcohol was in sufficient quantity to act as a physiological antidote to any poisonous element of the venom which it might have contained. We therefore made a further test of this matter by using Cobra venom, which is more powerful than that of the Crotalus, and using it in larger quantities.

Experiment.—Dissolved 0.1 gram Cobra venom in two drops of distilled water, and digested in 2.5 c. c. absolute alcohol for about ten days. The mixture was then filtered, and the filtrate evaporated spontaneously to  $\frac{2}{3}$  of a c. c. This was injected into a pigeon without any effect.

The following observations with Cobra venom are of great value as throwing light upon the different results obtained by various investigators in studying the action of alcohol on venom. In this series of experiments varying proportions of water were used to dissolve the venom.

Experiment.—Dissolved 0.02 gram dry Cobra venom in three drops of distilled water, then added 1 c. c. absolute alcohol and filtered.

- (I.) 4:37. Injected into the breast of a pigeon the above filtrate—no symptoms.
- (II.) 4:41. Injected the precipitate in a little water.

4:50. Dead.

Experiment.—Dissolved 0.03 gram Cobra in ten drops of distilled water and added 1 c. c. absolute alcohol and filtered.

- (I.) 5:00. Injected the filtrate as above.
  - 5:30. Sick
  - 5:53. Unable to stand; extremely feeble.
  - 5:55. Dead.

(II.) 5:05. Injected the precipitate with water. 5:07½. Dead.

In the first series the results are the same as in previous experiments, but in the second series, where a much larger quantity of water was used, the filtrate caused death in fifty-five minutes, thus proving that if sufficient water be present, enough of the poison is carried with the filtrate to cause death, notwithstanding the larger amount of alcohol present and its attributed antidotal action.

The Action of Absolute Alcohol upon the Dried Venom.—If dried venom be placed in absolute alcohol and the mixture allowed to stand for some time, even for months, it will be found that the venom undergoes no change in its poisonous activity, nor does it appear that the alcohol dissolves out any of the poisonous principles, since it is found to be innocuous after injection, and does not give any reaction for proteids.

The Effect of the Caustic Alkalies on the Toxicity of Venoms. Caustic Potash.—When caustic potash is added to a solution of venom the latter becomes perfectly clear. If the quantity of salt added to the solution is below a definite limit no decided alteration in the capacity to kill is noticed, but as this quantity increases obvious results are observed, first a diminution in the activity of the poison, and at last a complete loss of toxicity.

Experiment.—Dissolved 0.03 gram dried Crotalus adamanteus venom in 1 c. c. of distilled water in which was previously dissolved 0.0037 gram potassic hydrate.

3:45. Injected into the breast of a pigeon.

4:48. Weak.

5:00. Unable to walk; 6:00 ditto.

6:30. Dead. Heart arrested in systole; no ecchymoses; well-marked local effect; blood fluid at the end of sixteen hours.

Experiment.—The same as above, using 0.0075 gram potassic hydrate.

3:43. Injected.

5:00. Weak.

6:00. Weaker; slight local effect.

Following morning. Animal living, but weak; the local effect is well marked.

Experiment.—The same, using 0.015 gram potassic hydrate.

3:47. Injected.

7:00. No symptoms up to this time.

7:30. Sickish.

Following morning. Sickish; some slight local effect at point of injection.

Experiment.—The same, using 0.03 gram potassic hydrate.

3:50. Injected.

7:00. No symptoms up to this time.

Following morning. No symptoms; no local effects.

This experiment was repeated in two other pigeons with a like result.

The last series of experiments prove clearly that the addition of potassic hydrate to a solution of venom, if in sufficient quantity, produces a decided effect on the activity of venom, and that if added to the venom of the *Crotalus adamanteus* in a quantity equal to the weight of the dried poison the lethal action is entirely destroyed. In one experiment made with the venom of the *Crotalus horridus* the

same holds good, but our experiments with Cobra venom show that a larger proportional quantity is needed to destroy its power.

Experiment.—Dissolved 0.015 gram Cobra venom in 0.5 c. c. distilled water, then added an equal amount of potassic hydrate.

- 4:05. Injected into the breast muscles of a pigeon.
- 4:22. Unable to stand.
- 4:32. Convulsions.
- 4:37. Dead.

This experiment was repeated with a similar result.

A larger proportion of the potassic hydrate was used in the following observations:—

Experiment.—The same as above, using 0.03 gram (double the amount) of potassic hydrate.

4:51. Injected into the breast of a pigeon.
No effects.

Repeated this experiment with a similar result.

In one instance, however, we found that 0.06 gram potassic hydrate did not effectually counteract the poisonous activity of 0.015 gram dried Cobra.

It has been suggested that the non-poisonous action of venom treated with potassic hydrate and injected hypodermically, as in the above experiments, depends upon an effect of the potassic salt on the tissues, causing a considerable delay in the absorption of the poison, and this suggestion seems strengthened by the result in a rabbit of an *intravenous* injection of 0.015 gram Crotalus venom with 0.06 gram potassic hydrate in 1 c. c. distilled water. The animal became very sick soon after the injection, which was given in the evening, and remained in this condition at the end of an hour, when the observation ceased. The following morning it was found dead, with post-mortem appearances of the effects of venom. Also, in another animal, which was given intravenously 0.015 gram of venom with a similar amount of potassic hydrate, death occurred as promptly as with pure venom; in fact rather earlier.

In another set of experiments on pigeons, we carefully neutralized the potassic hydrate before injecting. We used in all of this series sulphuric acid as the neutralizing principle, so that a harmless potassic sulphate was formed. The results of this group of experiments also go to show that the potassic hydrate prevents the absorption of the venom.

Experiment.—Dissolved 0.015 gram dried venom of the Crotalus adamanteus in 1 c. c. distilled water and added 0.015 gram potassic hydrate, then carefully neutralized with acetic acid.

This was injected into the breast of a pigeon, causing death in sixteen minutes. Experiment.—Dissolved 0.03 gram dried Crotalus adamanteus venom in 1 c. c. distilled water and added 0.015 gram potassic hydrate, and then neutralized as above.

4:19. Injected as above.

4:55. Weak; breathing rapid.

6:20. Much weaker.

Following morning. Dead. Decided local effect; blood fluid and dark.

Experiment.—The same, only using 0.0075 potassic hydrate.

4:53. Injected as before.

5:00 Weak; breathing deep.

5:10. Dying.

5:18. Dead. Slight local effect; blood fluid and dark.

The records of the above experiments, which are in accord with Wall's, show that the results after the addition of the potassic hydrate are not the same as in the series where the alkali was not neutralized, thus proving that the effect of the action of the added alkali does not remain after the latter is neutralized.

In previous observations we found that solutions of venom were more or less impaired by boiling, and that this was particularly marked with the venom of the *Crotalus adamanteus*, 0.015 gram being rendered completely innocuous to pigeons. It was afterwards found that no coagula were formed by heating solutions of venom to which had been added some potassic hydrate, as in the above experiments. This led us to study the results of heating solutions of venom to which the potassic hydrate was added to learn if heat was capable of destroying or impairing toxicity without the occurrence of coagulation as a necessary event.

Experiment.—Dissolved 0.015 gram of the venom of the Crotalus adamanteus in 1 c. c. distilled water and added 0.015 gram potassic hydrate, and subjected the solution, as in previous experiments, to a gradually increasing temperature up to 74° C. It was then injected into a pigeon. At the end of twenty-four hours there was no effect.

In this experiment the temperature to which the solution of venom was submitted was below the point at which serious impairment of the poisonous power of the venom occurs, yet the amount of potassic hydrate was sufficient to destroy its action. Other experiments were made in which the quantity of potassic hydrate was not sufficient to effect this end. We found in previous experiments that 0.0037 gram potassic hydrate was not sufficient to destroy the toxicity of 0.03 gram of *Crotalus adamanteus* venom, although the time of the occurrence of death was considerably delayed.

We used similar amounts of venom and alkali in the three following experiments, using 0.5 c. c. distilled water for the solutions.

Experiment.—Dissolved 0.09 gram of Crotalus adamanteus venom in 1.5 c. c. distilled water and added 0.011 gram of potassic hydrate. This solution was divided into three parts. One of which was heated to 76.5° C., one to 79.5° C., and the other to 83.5° C. Each of which was injected into the breast of a pigeon and without any evil consequence following within twelve hours.

These results indicate that heat impairs the poisonous activity of venom under the above conditions, even though coagulation does not occur. In previous experiments recorded it was found that at a temperature of 79.5° 0.03 gram of *Crotalus adamanteus* venom was rendered non-toxic. The explanation of the further impairment of the action of the poison by heating its solutions having potassic hydrate dissolved in them lies probably in the fact that the potassic hydrate is placed by heat under condition of greater activity. The non-coagulability of solutions of venom to which potassic hydrate was added is no doubt due to the alteration

of the coagulable proteids into alkali-albumins, and as a moderate degree of heat increases the rapidity of this change, it is possible that the smaller amount of alkali is as effective under these conditions as the larger amounts under ordinary conditions. It is not at all improbable that the prolonged action of potassium hydrate on solutions of venom may convert all of the globulins into alkali-albumins and thus destroy their poisonous activity.

Sodic Hydra'e.—The effect of sodic hydrate on solutions of the venoms of the Crotalus adamanteus and horridus appears to be the same as that of the potassic salt. In one experiment with the Crotalus adamanteus, using equal quantities (0.03 gram) of the dried venom and alkali, no poisonous effects followed its injection; and in another experiment in which 0.015 gram of venom and 0.007 gram sodic hydrate were used the animal was rendered somewhat sick, but fully recovered.

In one experiment with the venom of the *Crotalus horridus*, using equal quantities (0.015 gram) of the venom and sodic hydrate, no poisonous symptoms followed.

The effect on solutions of dry Cobra venom, as in the case of the potassic salt, is not so marked.

Experiment.—Dissolved 0.015 gram dry Cobra venom in 0.5 c. c. distilled water and added 0.015 gram sodic hydrate.

4:08. Injected into the breast of a pigeon.

4:15. Unable to stand.

4:27. Dead.

In two other experiments, using double the quantity of sodic hydrate, one animal died in one hour, and the other in a little less than three hours. Double amounts therefore decidedly impair toxicity. In another experiment, in which four times the quantity of sodic hydrate was used (0.015 gram dried venom + 0.06 gram NaHO), no poisonous symptoms followed.<sup>1</sup>

The Effects of Ammonia.—The dry venom of the Crotalus adamanteus, which was the only one used, forms with aqua ammonia a turbid solution, such as is formed with water. The effect on the toxicity of the venom exerted by the ammonia is not so marked as with the potassic or sodic hydrates.

Experiment.—Dissolved 0.03 gram dried venom in two minims aqua ammonia (20°) with 1 c, c, distilled water,

5:29. Injected into the breast muscles of a pigeon.

5:37. Unable to walk.

5:46. Convulsions; death. The local lesions are decidedly lessened by the alkali.

Experiment.—The same, using six minims aqua ammonia.

4:14. Injected as above.

6:00. No marked symptoms up to this time, excepting droopiness. The local effect is slightly more marked than in No. 1.

Following morning the animal was dead.

In three other experiments in which eight minims of aqua ammonia were used two of the animals were found dead the following morning and one recovered. In

<sup>&</sup>lt;sup>1</sup> See Shortt. Wall, op. cit., p. 133. On the effects of alkalies and of permanganates, see Vincent Richards, F.R.C.S. Ed., etc., op. cit.

another experiment in which the alkali was neutralized by sulphuric acid, death did not occur for four hours.

In the first experiment, in which a very small amount of ammonia was used, death occurred in less than twenty minutes; in the next, in which three times the quantity of ammonia was used, death did not ensue for some hours, while in the next three a more positive effect was no doubt apparent in the fact that one of the pigeons recovered. In the last experiment death did not occur for over four hours, even after neutralization of the alkali, indicating, as in the case of the potassic hydrate, that some permanent effect had been exerted on the venom by the ammonia.

Potassium Carbonate.—Two experiments made with the venom of the Crotalus adamanteus render it probable that the potassic carbonate does not exert any decided effect.

Experiment.—Dissolved 0.015 gram venom in 1 c. c. distilled water and added 0.015 gram potassic carbonate.

4:16. Injected into the breast of a pigeon.

4:22. Down.

4:25. Dead. No appreciable local effect.

Experiment.—Dissolved 0.03 gram venom in 1 c. c. distilled water and added 0.12 gram potassic carbonate.

5:25. Injected into the breast muscles of a pigeon.

5:45. Down; observation now ceased.

Following morning found dead; slight local effect.

Nitric Acid.—The powerful destructive action exerted by this acid on albuminoids suggests at once that it would in all likelihood completely destroy the poisonous properties of venom, yet it has been asserted that such is not the case. In the latter instance the result was no doubt due to the insufficiency of acid used, as we have clearly determined in our experiments.

Experiment.—Dissolved 0.03 gram Crotalus adamanteus venom in 0.5 c, c, distilled water and added  $2\frac{1}{2}$  minims C. P. nitric acid, which caused a considerable precipitate.

3:32. Injected the above into the breast of a pigeon.

3:33. Convulsions, followed by death.

From this result it seemed probable that not enough acid had been added to throw down all of the precipitable proteids. In another experiment the acid was added to a solution of venom and the mixture filtered. The filtrate was now tested with nitric acid and a further precipitate occurred. This process was repeated until no further precipitate followed. The filtrate was set aside, and the precipitate on the filter washed with dilute nitric acid and then with water.

Experiment.—5:05 injected into the breast of a pigeon the above filtrate, which measured 3 c. c. and contained 1 c. c. nitric acid.

6:05. No symptoms except slight droopiness.

Following morning no effects from venom.

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Experiment.—5:55 injected the precipitate in 1 c. c. dilute nitric acid with which it had been in contact for two hours.

6:05. No symptoms. Following morning animal in good condition.

It will thus be observed that the acid has completely destroyed the toxicity of venom. We made still another experiment in which the venom was rubbed up in a mortar and the acid added to it, and then diluted with water.

Experiment.—0.03 gram dried Crotalus venom was rubbed in a mortar until powdered, and 4 gtt. C. P. nitric acid added. This formed a pasty mass of an orange-yellow color. With 1 c. c. distilled water it formed a cloudy, orange-yellow solution.

The above was injected into the flank of a half-grown rabbit, without any symptoms of venom poisoning following within twelve hours.

A similar experiment was made with a pigeon with a like result. The acid, however, having been neutralized with sodic carbonate before injection.

Muriatic Acid.—This acid does not seem to exert so strong an effect. Only one experiment was made.

Experiment.—0.015 gram dried Crotalus venom was rubbed in a mortar, and to it was added 4 gtt. C. P. muriatic acid forming a clear solution. With 1 c. c. distilled water it made a turbid solution.

3:44. Injected the above into the breast muscles of a pigeon.

5:00. Very sick.

5:50. Nearly dead.

Following morning dead; no local lesions from venom.

Here the amount of venom used was only one-half of that employed in the nitric acid experiment. The quantity of acid was the same, but in this experiment a pigeon was used.

As in the series with nitric acid, an experiment was also made in which the dried venom was powdered in a mortar and a few drops of the pure acid used. About 1 c. c. of distilled water was added, and the mixture neutralized with sodic carbonate. It was then injected into the breast of a pigeon with the result of death in twenty-six minutes.

Sulphuric Acid.—Repeated the above, using instead of the muriatic acid 5 gtt. sulphuric acid. The venom and acid formed a clear syrupy solution which became milky by the addition of the water.

3:53. Injected as above.

5:50. Sickish.

Following morning dead; no local symptoms of venom poisoning.

Dr. Mitchell had observed that if the acid was afterwards neutralized the action of the venom was not affected. The delay of death in this experiment seems to be due to the action of the non-neutralized acid. We, however, made an experiment by powdering the dried venom (0.015 gram) in a mortar, adding a few drops of the pure acid, diluting then with about 1 c. c. distilled water, and neutralizing with sodic carbonate. This was injected into the breast of a pigeon.

For some time after the injection the bird was weak, and continued in a feeble condition until eighteen hours after the injection, when death ensued.

It seems quite remarkable that such a powerful acid as sulphuric does not completely destroy the poisonous properties of the venom, and it is even more curious that pure muriatic acid seems to be without effect.

Acetic Acid. Experiment.—Dissolved 0.02 dried venom (Crotalus adamanteus) in 0.1 c. c. distilled water and added 3 minims of glacial acetic acid.

- 4:30. Injected into the breast of a pigeon.
- 4:37. Incoördination.
- 4:41. Dead.

Death occurred in this experiment in such a short time that it was thought that the acid itself might have contributed to this end. We therefore made another experiment in which the acid was neutralized.

Experiment.—Prepared the venom as before, only neutralizing the solution with sodic carbonate.

- 4:35. Injected into the breast of a pigeon.
- 5:10. Pigeon unable to stand.
- 5:15. Dead.

The result of this experiment indicates that the presence of the free acid aids the toxic action of venom.

Hydrobromic Acid. Experiment.—Powdered 0.015 gram dried Crotalus adamanteus venom in a mortar and added 5 gtt. hydrobromic acid (sp. gr. 1.274), after five minutes added 0.5 c. c. distilled water. The venom and acid formed a slightly reddish-colored solution, which became milky when diluted with water.

- 4:25. Injected into the breast muscles of a pigeon.
- 4:45. Sickish.
- 4:55. Unable to stand. (Final result not noted, but death most certainly followed.)

We repeated the above experiment, using 10 gtt. of acid mixed with an equal part of water, before dissolving the venom in it.

- 2:49. Injected as above.
- 3:07. Rocking.
- 3:30. Dead; local effects of the venom apparent.

Notwithstanding we used double the amount of acid in this experiment, it does not appear as though the activity of the venom was made to differ much from that noted in the previous experiment. Since the previous dilution of the acid before mixing with the venom might have affected its action a third experiment was made in which the same quantity of acid was added, without dilution, to the powdered venom.

Experiment.—Powdered 0.015 gram dried venom and added 10 gtt. hydrobromic acid, then 1 c. c. distilled water.

- 4:20. Injected the above into the breast muscles of a pigeon.
- 5:00. No apparent effect.
- 5:10. Sickish.
- 6:00. Siekish.

Following evening. Well.

This last experiment was repeated with the modification of leaving the acid in contact with the venom for one-half hour before the addition of the water. It was then injected as above without any obvious effects following.

The destructive action of the acid on the venom of the *Crotalus horridus* seems to be the same if we can judge from the single experiment which follows.

Experiment.—Powdered 0.015 gram dried venom and added 10 gtt. hydrobromic acid, which formed a muddy solution with a reddish color.

5:18. Injected into the breast of a pigeon without any obvious effects within twenty-four

The effect on the activity of Cobra venom, using similar quantities of venom and acid is very different.

Experiment.—Repeated the above, only substituting Cobra venom.

4:48. Injected into the breast muscles of a pigeon.

5:18. Sick; breathing difficult.

5:30. Breathing more difficult; convulsive movements; incoördination.

5:35. Dead.

Tunnic Acid.—The action of tannic acid upon albuminoids is so decided that we might confidently expect, since we find the poisonous elements in venoms to be proteids, that the activity of venom would be greatly diminished or entirely destroyed by it. In one experiment made with the venom of the Crotalus adumanteus we found comparatively little effect.

Experiment.—Dissolved 0.03 gram dried venom in a little distilled water and added 1.5 c. c. saturated solution of tannic acid.

3:35. Injected into the breast muscles of a pigeon.

4:00. Droopy.

4:45. The same. Following morning dead.

It will be observed that there is a great delay in the action of the venom, possibly due to the powerful local constrictive action of the tannic acid on the tissues, and possibly, also, to a direct action of the acid on the venom itself. As death may have resulted from the tannic acid we made a control experiment in which 1.5 c. c. saturated solution was injected into the breast of a pigeon. The animal did not exhibit any signs of active poisoning, but it died at the end of the fourth day.

Alum.—We made but two experiments with alum, one with the venom of the Crotalus horridus and one with Cobra.

Experiment.—Dissolved 0.015 gram dried venom in 0.5 c. c. distilled water and added 3 gtt. saturated solution of alum (18° C.), but no precipitate occurred; we then gradually added powdered alum nearly to saturation, which caused precipitation. The precipitate was filtered off, and the clear filtrate tested by the further addition of alum to see if any more precipitation would occur, with a negative result. The precipitate and filtrate were now mixed together and injected into the breast of a pigeon without any poisonous result occurring within forty-eight hours.

In another experiment in which 0.06 gram of dried Crotalus venom was used, the animal died in forty-five minutes.

Alum added to saturation does not precipitate the peptone, although it precipitates all of the coagulable proteids.

The following is the experiment with Cobra venom:-

Experiment.—Dissolved 0.015 gram dried venom in 0.5 c. c. distilled water and added alum to saturation (16° C.).

4:32. Injected into the breast muscles of a pigeon.

4:50. Down.

4:52. Dead.

This last experiment is of interest in proving that even so powerful an astringent as alum is not sufficiently strong to prevent the prompt absorption of the poison. Death followed in twenty minutes.

Chlorine Water.—This reagent does not seem to exert any influence.

Experiment.—Dissolved 0.015 gram Crotalus adamanteus venom in 0.5 c. c. distilled water and added 0.5 c. c. fresh chlorine water.

4:28. Injected into the breast muscles of a pigeon.

4:52. Down.

5:10. Dead.

Bromine.—The action of bromine in bromohydric acid solution is very marked. Experiment.—Powdered 0.015 gram dried Crotalus adamanteus venom in a mortar and added 2 gtt. of bromine in 4 or 5 gtt. bromohydric acid, then added 0.5 c. c. alcohol.

5:05. Injected into the breast of a pigeon.

5:30. No effect.

Twenty-four hours. No effect.

This experiment was repeated once with Crotalus venom and once with Cobra, using water as the diluent instead of alcohol. In both experiments we found a similar result, thus proving that the activity of the venom is completely destroyed by this reagent.

Iodine. Experiment.—Dissolved 0.015 gram dried venom of Crotalus adamanteus in 0.33 c. c. distilled water, then added 0.5 c. c. tr. iodine which formed a dense brown precipitate.

5:07. Injected into the breast of a pigeon.

No poisonous effects within twenty-four hours.

If, however, the amount of iodine be much smaller the venom is still potent, as is shown by the following experiment.

Experiment.—Dissolved the venom as above, then added 1 drop tr. iodine and afterwards 1 c. c. distilled water.

4:56. Injected into the breast of a pigeon.

5:05. Weak.

5:15. Dying.

Iodine + Potassic Iodide. Experiment.—Dissolved 0.015 gram dried venom of Crotalus adamanteus in 0.5 c. c. distilled water, then added a saturated solution of equal parts of tr. iodine and potassic iodide.

4:41. Injected the above into the flank of a small rabbit (half grown). The animal died in about eighteen hours.

The delay in the occurrence of death in this experiment was considerable, and that this was due to the action of the iodine on the venom is rendered probable by the results of the preceding experiments with iodine and by the following experiment with the potassic iodide.

Potassic Iodide.—This salt does not seem to exert any influence upon the activity of venom.

Experiment.—Dissolved 0.015 gram dried venom of the Crotalus adamanteus in 1 c. c. saturated solution of potassic iodine.

- 4:31. Injected into the breast of a pigeon.
- 4:40. Down.
- 4:45. Dead.

Potassic Bichromate. Experiment.—Dissolved 0.03 gram dried Crotalus adamanteus venom in 1 c. c. distilled water and added 0.01 gram potassic bichromate.

- 4:14. Injected into the breast of a pigeon.
- 4:20. Down.
- 4:25. Convulsions followed by death.

Experiment.—Dissolved 0.004 gram dried venom in 0.5 c. c. distilled water and added 0.03 gram potassic bichromate dissolved in 0.33 distilled water, which produced a dense coagulum.

- 3:38. Injected into the breast muscles of a pigeon.
- 4:05. Dead.

Potassic Permanganate. Experiment.—Dissolved 0.03 gram dried Crotalus adamanteus venom in 0.5 c. c. distilled water and added 0.06 gram permanganate in 0.5 c. c. distilled water. This formed a very cloudy solution.

5:27. Injected into the breast of a pigeon. Death occurred within forty-eight hours.

Experiment.—The same, using 0.015 gram of the permanganate. At the end of the second day no poisonous effects from the venom. The parts where the injection was made look as though they would slough.

Experiment.—The same, using 0.005 gram of the permanganate. The solution formed is a dark wine color.

4:37. Injected into the breast of a pigeon without effect.

Experiment.—The same, using 0.0038 gram of permanganate.

- 4:26. Injected as above.
- 4:42. Down.
- 4:45. Dead.

Experiment.—The same, using 0.0025 gram of permanganate.

- 3:57. Injected as above.
- 4:06. Down.
- 4:10. Dead.

In another experiment, the mixture was injected into the femoral vein of a rabbit, using 0.005 gram permanganate. The animal lived, and at the end of the second day was apparently unaffected.

In one observation made with the venom of the *Crotalus horridus* 0.015 gram of venom was dissolved in 0.5 c. c. distilled water, to which was afterwards added 0.008 gram of the permanganate. After standing for twenty-four hours the

mixture was very thick and tarry, and would not flow from the inverted test-tube. It seems from this that the full extent of the action of the permanganate on the venom is not exerted for some hours.

The permanganate is efficient in destroying the activity of Cobra venom.

Experiment.—Dissolved 0.015 gram dried Cobra venom in 0.5 c. c. distilled water and added 0.015 gram permanganate.

4:35. Injected into the breast muscles of a pigeon. No symptoms of venom poisoning within twenty-four hours.

Peroxide of Hydrogen.—Notwithstanding the powerful nature of the peroxide of hydrogen as an oxidizer, it does not seem to affect to any great extent the poisonous activity of venom. Only one experiment was made.

Experiment.—Added 3 drops of fresh venom of the Crotalus adamanteus to 3 c. c. fresh solution of peroxide of hydrogen, specially prepared by Prof. Leeds, of Hoboken.

- 5:05. Injected into the breast muscles of a pigeon.
- 5:15. Unable to stand; decided local effects appearing.
- 6:05. Dead, with all the usual phenomena of venom poisoning.

The quantity of peroxide of hydrogen used in this experiment was so large that the test was a satisfactory one.

Argentic Nitrate.—Notwithstanding the powerful action of nitrate of silver on albuminoids it does not seem to possess great power to disturb the toxicity of venom.

Experiment.—Dissolved 0.015 gram of dried venom of Crotalus adamanteus in 3 c. c. distilled water, to which was afterwards added 0.015 gram nitrate of silver, forming a decidedly milky solution.

- 4:40. Injected into the breast of a pigeon.
- 4:50. Down; deep breathing, gasping.
- 4:53. Dead.

As there was a possibility of the quantity of salt being insufficient for the amount of venom, another experiment was made in which double the weight of nitrate was used. The mixture was injected into the breast of a pigeon. At the end of three days no symptoms of venom poisoning had occurred.

Mercuric Chloride.—When mercuric chloride is added to a solution of Crotalus or Moccasin venom a dense precipitate occurs, consisting of all the proteids in solution. In order to learn if the precipitated proteids still retained any toxic power we dissolved 0.03 gram of dried venom of the Crotalus adamanteus in 1 c. c. distilled water and then added 0.03 gram mercuric chloride. The precipitate was collected on a filter and repeatedly washed with distilled water. During this washing the precipitate seemed to diminish a little in quantity, and was no doubt partially dissolved.

- 3:30. The precipitate in 1 c. c. distilled water was injected into the breast of a pigeon.
- 6:00. No symptoms up to this time.

Twenty-four hours-the animal showed no signs of venom poisoning.

Ferrous Sulphate.—Three experiments were made with the sulphate of iron with results materially different; the difference no doubt depending upon the mode

of administration. In all the same quantities of venom and salt were used, but in one the solution was injected simply beneath the skin and in the others directly into the muscles of the breast. In the former the animal did not die until after the lapse of nearly thirty-six hours, while one of the others died remarkably soon—within four minutes after the injection, and the third in twenty-eight minutes.

Experiment.—Dissolved 0.03 gram dried venom of the Crotalus adamanteus in 1 c. c. distilled water and then added 0.03 gram ferrous sulphate. The addition of the iron salt renders the solution clear.

3:40. Injected beneath the skin of the thigh of a pigeon.

6:00. No apparent effects.

Twenty-four hours—no effects. Thirty-six hours—dead. Slight local effects of venom, but the destructive action of the iron salt on the tissues is much more prominent.

Experiment.—The same as above.

3:32. Injected into the breast muscles of a pigeon.

3:36. Convulsions; death. No local lesions.

In another experiment the bird died in twenty-eight minutes after injection.

It must be concluded from this that the ferrous sulphate does not destroy the activity of the venom.

Dialyzed Iron.—When dialyzed iron is added to a solution of venom all of the proteid matter is precipitated, and the filtrate is found to give no reaction for proteids with the xanthoproteic or picric-acid tests. The precipitate is brown, and so gelatinous that if the solutions are somewhat concentrated it does not flow. The precipitate does not dissolve in distilled water, yet it must be very soluble in the tissues since the toxic effects of the venom rapidly appear after its injection. We made two experiments, both with Moccasin venom, one with the dried and the other with fresh venom.

Experiment.—Dissolved 0.015 gram dried Moccasin venom in 0.5 c. c. distilled water and added 3 gtt. dialyzed iron. This caused a considerable amount of brownish gelatinous precipitate which thickened the mixture appreciably. Now added 1 c. c. distilled water.

3:20. Injected into the breast muscles of a pigeon.

3:25. Down.

3:45. Dead.

Experiment.—Took two drops of fresh Moccasin venom and added first 5 gtt. dialyzed iron, and then 1 c. c. distilled water. The iron and venom made a very thick brownish mixture.

5:18. Injected into the breast muscles of a pigeon.

5:30. Dead.

One experiment was made in this connection to see if dialyzed iron exerted any poisonous effect, we injected thirty drops into the breast muscles of a pigeon, without toxic result.

Ferric Chloride.—We have used the chloride of iron in two forms; the officinal tineture, U. S. P., and the officinal liquor. Both these solutions greatly affect the poisonous activity of venom, the latter, indeed, if used in sufficient quantity,

wholly prevents the occurrence of any of the symptoms of venom poisoning. The tincture does not appear to be nearly as efficient.

Experiment.—Dissolved 0.015 gram dried venom of the Crotalus adamanteus in 0.5 c. c. distilled water and added 10 gtt. tr. chloride of iron. As the iron was added the solution cleared, but in a few moments became milky, and finally thick

with whitish precipitate.

4:22. Injected into the breast of a pigeon.

5:00. No symptoms.

5:45. No symptoms.

Following morning-dead. No local effect.

In two similar experiments, in which double the quantity of the tincture of iron was used, the result was much the same, the time of death being notably delayed.

The following experiments were made with the liquor:-

Experiment.—Dissolved 0.015 gram dried venom of Crotalus adamanteus in 0.5 c. c. distilled water and added 4 gtt. liquor ferri chloridi. A heavy precipitate fell.

4:45. Injected into the breast of a pigeon.

5:00. Very quiet.

6:00. No symptoms, and none of venom poisoning within two days.

A similar experiment was made with identical results.

In one experiment with the venom of the *Crotalus horridus*, in which only two drops of the liquor were used, the animal showed no evidences of poisoning; and in four experiments made with the dried venom of the *Moccasin*, in which 0.015 gram of dried venom was used and eight, four, two, and one drop of the liquor were used, three animals gave no symptoms of venom poisoning, and one died on the third day—the animal receiving the injection containing but one drop of the iron. This was the only pigeon of the four which gave any signs of poisoning. In three-fourths of an hour the bird was shaky, and at the end of three hours decidedly feeble, remaining pretty much in this condition until death.

About the point of injection the iron produced considerable hardening of the

The effect on Cobra venom is not marked, although in one experiment there was an appreciable delay in the occurrence of death; but in the other, in which the quantity of iron was larger, death occurred with remarkable rapidity.

Experiment.—Dissolved 0.015 gram dried Cobra venom in 0.5 c. c. distilled water and added 2 drops liquor ferri chlor. A slight precipitate occurred in the solution after a few moments.

3:47. Injected into the breast muscles of a pigeon.

4:15. Convulsions.

4:27. Dead.

Experiment.—Dissolved 0.015 gram dried Cobra venom in 1 c. c. distilled water and added 5 gtt. sol. perchloride of iron.

This was injected into the breast of a pigeon, with the result of death in twenty seconds.

The reason why ferric chloride is inefficient in destroying the toxicity of Cobra venom no doubt lies in the fact of its main poisonous substance being a peptone,

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and, like that element in all the venoms, unaffected by the iron, while the principal toxic effects of the Crotalus and Ancistrodon venoms is due to the globulins which are precipitated and chemically altered by the iron salt.

Filtration through Various Substances.—Filtration through alumina or wood charcoal does not affect the poisonous activity of the venom, but by filtration through animal charcoal all of the poisonous material in venom is left behind and the filtrate is accordingly innocuous.

Experiment.—Dissolved 0.03 gram dried Moccasin venom in 2 c. c. distilled water and filtered four times through animal charcoal. The filtrate gives no proteid reaction.

4:20. Injected 1.5 c. c. of the filtrate into the breast of a pigeon. At the end of twenty-four hours no symptoms of venom poisoning had occurred, but there was some ædema at the point of injection.

Repeated the above experiment, using 0.045 gram of Moccasin venom, and with similar results.

Snake Bile.—Among the curious substances which have been extolled as antidotes for venom poisoning is snake bile. We made but one experiment, which speaks volumes.

Experiment.—Mixed  $1\frac{1}{2}$  minims of fresh venom from a dead Crotalus adamanteus with 1 c. c. of bile from the same animal.

- 4:47. Injected into the breast of a pigeon,
- 4:471. Incoordination.
- 4:50. Gasping respiration.
- 4:55. Convulsive movements.
- 4:56. Dead.

Digestion.—By digestion in strong artificial gastric juice made from the pig's stomach the toxic power of venom (Crotalus) is completely destroyed.

Experiment.—Three drops of the glycerine solution of venom (Crotalus horridus) (1862) were digested for sixteen hours in about 1 c. c. fresh artificial gastric juice from the pig's stomach.

8:30 A. M. Injected into the breast muscles of a pigeon. Up to the end of forty-eight hours no poisonous symptoms ensued.

This experiment was repeated with an identical result. We also made two experiments in which the digestive process was not carried on for such a length of time, in both only four hours, and with similar results. In one we used six drops of the glycerine solution of venom as above—just double the dose—and in the other 0.015 gram of the dried *Crotalus adamanteus* venom.

The results of digestion in artificial pancreatic juice are similar. We made but one experiment, and that with the venom of the *Crotalus adamanteus*.

Experiment.—Digested 0.03 gram dried venom in 1 c. c. freshly prepared pancreatic juice from the pig for twenty-four hours,

3:44. Injected into the breast muscles of a pigeon.

5:45. Slightly droopy.

Following morning, no effects apparent.

Résumé.—The above experiments, with others too numerous for detail, have enabled us to confirm Lacerda's and Vincent Richard's views as to the power of permanganate of potassium to destroy venoms. As a local antidote it is for all snake poisons the best.

It is also clear from what we have seen that ferric chloride is a very efficient local destroyer of the venom of our own snakes, which owe their vigor to venom-globulin, but has little value as a local antidote to the peptone which gives power to the poison of the Cobra. The chloride needs to be locally used in full doses, whence it is that the strong liquor ferri chloridi (U. S. P.) is more efficient than the tincture.

That bromine may prove valuable as a local means of relief seems to be plain from our experiments, and is in fact one of their most interesting results. It was used, as we have seen, either as hydrobromic or bromohydric acid. Probably any solution of bromine would answer, and—as was shown by its free local use to control gangrene during our civil war—there need be no fear in using it with freedom.

It has long been known in India that the strong alkalies destroy venom, and this we are able to confirm. Brainerd long ago taught that iodine has destructive value as regards Crotalus venom, and this also seems to us to be true.

In fact many agents more or less alter venoms if allowed to remain long in contact with them, and usually act with increased vigor as the temperature is raised above that of the air; but it is chemically singular that brief exposure of venoms to strong acids should so little affect the toxicity of the poisons in question. Except where otherwise distinctly stated, the chemicals used by us have been added to the poison immediately before injecting it. Enough has been here proved to make it now worth while to study still more carefully the value of bromine and ferric chloride as local poison destroyers. One agent may be at hand or available when others are not, and the more numerous are the means we possess as local antidotes the better is the chance of escape or relief for persons bitten.

#### CHAPTER IV.

# THE EFFECTS OF VENOM WHEN APPLIED TO MUCOUS OR SEROUS SURFACES.

The Effects of Venom when applied to Mucous Surfaces.—The question of the absorption of venom by mucous surfaces is one of great interest, and the verdict of all observers in connection with the venom of the Crotalidæ is that uninjured mucous surfaces, except in the lungs, cannot absorb venom, at least in sufficient quantities to produce death. In experiments with the venom of the Cobra other investigators have gotten results which are directly contrary, but in our own researches a large proportion of the animals survived.

In seven experiments made on pigeons, in which a solution of Cobra venom was placed in the craw by means of an œsophageal tube, six showed no evidences of poisoning and one died. In these experiments the œsophageal tube, which was a small catheter, was oiled and passed with great care into the crop, the solution of venom was then poured through the tube by means of a funnel, and afterwards washed down with a little water.

Experiment.—Dissolved 0.025 gram dried Cobra (Naja trip.) in about 1 c. c. distilled water, and placed it in the crop of a pigeon by means of an œsophageal tube. Up to four days the animal showed no signs of poisoning.

Five other experiments, like the above, gave identical results. In one experiment the animal died within twelve hours.

Experiment.—Dissolved 0.013 gram dried Cobra (Naja trip.) in about 1 c. c. distilled water and gave to a pigeon, as above, at 4:00 p. m. A little while after the dose the pigeon appeared sickish and remained in much the same condition for about two hours, when observation temporarily ceased. At 8:30 the following morning the bird was dead. The heart was found in systole and contained dark clots. The blood was everywhere coagulated. No apparent lesions were present in any part of the body, and a most careful examination of the mouth, gullet, and crop revealed no abrasions or other raw surface. The crop contained a little cracked corn and a small amount of yellowish fluid.

In another pigeon, etherized, an opening was made through the skin into the craw, and its contents washed out. The pigeon was kept on its back and the edges of the wound were held up by retractors. A solution of venom was placed in the cul-de-sac on the left side and the animal watched. In a half hour the bird had convulsive seizures, and at the end of forty minutes was dead. At that time there seemed to be about the same quantity of venom solution in the crop as before. It was, however, somewhat glutinous and darker in color. The mucous

membrane preserved its natural tint. On the side in which was the poison the mucous membrane was wrinkled and raised in points like the surface of a mulberry. By stretching the mucous membrane this roughness disappeared. After death it increased somewhat. There was no ædema.

Experiment.—0.01 gram of dried Cobra dissolved in a little water was given to a frog by an œsophageal tube as in the case of the pigeons. The frog presented no toxic symptoms for two hours. After twelve hours it was dead.

Autopsy.—All the tissues had a cyanotic appearance and the animal was perfectly flaccid. The heart was still irritable as well as the intestines. The stomach contained a viscid mass of mucus, which was not bloody, and which was expelled from the stomach by the normal contractility when the organ was cut. A most careful examination of the mouth, gullet, and mucous membrane of the stomach did not reveal any abrasions or other raw surface. The liver seemed pale and decidedly friable.

In Dr. Mitchell's former experiments made in the opened crop, fatal results did not occur with use of fresh or dry venom of Crotali; but a single needle pricked through the mucous surface covered by the poison, sufficed to let in death.

It seems possible that minute ulcers or abrasions, quite invisible to the eye, might, in like manner, enable the venom in some cases to pass the barrier of the intestinal mucous lining. The deaths from ingested Cobra venom related by Fayrer took place in mammals, and we ourselves found in like experiments with rabbits, that, although death was rare after swallowing Cobra venom, it was less so than in pigeons; but our Cobra experiments are not strictly comparable with those done in India with fresh poison.

Certainly Cobra venom is much more apt to kill when swallowed than is Crotalus poison. In the rattlesnake it is the globulins which are in largest amount, and which are not dialysable, but in Cobra the fatal peptone is the material which, both as to vigor and amount, represents the poisoning capacity, and is as we know dialysable. It is only astonishing, therefore, that it does not kill in every case in which it is swallowed; but, as we have seen, the gastric juices in so far as they have time to act are destructive of venoms, and hence their protective agency has also to be considered.

The Activity of Venom when applied to Serous Surfaces.—One of the most remarkable and interesting of the physiological effects produced by the venom of the Crotalus is the occurrence of ecchymoses, especially in the serous tissues. The character of these ecchymoses is fully treated in another part of the work, so that we need here only detail some of our observations in connection with the direct effect of the application of venom to the serous tissues.

A rabbit was etherized and kept in this condition during the whole of the experiment. The abdominal cavity was opened and a knuckle of intestine exposed. On the peritoneum were placed a few small particles of the dried venom of the *Crotalus adamanteus*. In two or three minutes some extravasations appeared immediately about the point of the application of the venom; a few moments later these extravasations were diffused over a considerable area and had run into each other to such an extent as to form a patch of bleeding surface. So

rapidly do these hemorrhages spread that they can literally be seen to grow under the eye. Another portion of the intestine was exposed, and upon the peritoneum was placed a very small portion of the glycerine solution of venom (prepared in 1862), which has already been referred to. Ten minutes after the application small points of extravasation appeared, and in three minutes more had increased so much in number and spread so rapidly as to form a continuous area of bleeding surface. Four drops of the glycerine solution of venom in a little water were boiled and carefully evaporated to a thick paste and then applied to a fresh surface of the peritoneum. After one hour no ecchymoses appeared.

In another experiment 0.03 gram of the dried Moccasin venom was boiled and injected into the peritoneal cavity of a pigeon. The animal died in forty-two minutes, when we found large ecchymoses scattered over all the abdominal viscera. In later experiments we have fully determined that the venom peptone may cause ecchymoses, but that this power exists in an insignificant degree as compared with that of the globulins.

In another experiment, not irrelevant here, we injected one drop of the fresh venom from the *Crotalus adamanteus* into one of the mesenteric arteries of an etherized rabbit. In a few seconds ecchymotic patches appeared on the large intestine followed by a few on the small intestine, and in another moment the animal was dead.

In an experiment on an alligator, elsewhere quoted, the activity with which venom may be absorbed by serous membranes is well illustrated. In a frog death occurred within two hours after the injection of two drops of the fresh venom of the *Crotalus adamanteus* into the peritoneal cavity.

In one experiment made upon an etherized rabbit in which 1 drop of fresh Moccasin venom was dissolved in 1.5 c. c. of distilled water and injected into the peritoneal cavity the animal died in one and a quarter hours. In an autopsy one hour after death, it was found that there was no rigor mortis; the whole of the inside of the peritoneal cavity was stained, and in places was literally dripping with blood; the mesentery contained a large amount of blood resembling a free clot. On the surface of the intestines the effusion of blood was of a brilliant red color as though from the arterioles; the whole interior of the abdominal cavity was stained; the heart was arrested in systole.

In still another experiment in which the solution of venom was boiled the results were strikingly different. We dissolved 0.03 gram of dried Moccasin venom (representing a much greater dose than was given in the previous experiment) and after boiling it for a moment filtered it. The filtrate was injected into the peritoneal cavity of a rabbit. The animal was killed after the lapse of one hour and the peritoneal cavity examined. There were absolutely no alterations to be seen in the viscera, excepting one minute spot where there appeared a little reddening.

The length of time during which the venom used was boiled was not distinctly stated in the notes of some of our observations. The omission was of moment.

At the time these experiments were made, we did not fully know that while in all venoms—brief boiling throws down the globulins at once—much longer boiling by degrees precipitates, and at last makes innocent the peptones. Apparently it

is the globulins which most rapidly alter blood and vessels, and by a mechanism hereinafter to be described cause ecchymoses. Yet are the peptones not without this toxic capacity, as is seen in some of the above observations. Clearly, however, boiling impairs the activity of Crotaline peptones, as it does that of like constituents of Cobra poison. It will have been seen that none of these direct experiments on serous tissues were made with pure or boiled Cobra venom. It is desirable that this should be done, and especially with fresh venom. In another portion of this paper there are some relative studies of the power of dried Cobra and Rattlesnake venoms to cause local hemorrhages from the peritoneum. In the former work of Dr. Mitchell, and in that of Fayrer and Brunton, are sufficient studies of the absorbing power of rectal and pulmonary surfaces and of the eye.

#### CHAPTER V.

#### THE EFFECTS OF VENOM ON THE NERVOUS SYSTEM.

EXCEPTING as regards the marked action on the respiratory centres we cannot consider venom as essentially or solely a nerve poison. In animals which do not immediately die from the effects of this poison, the first signs of nerve poisoning are drowsiness, incoördination, followed by loss of voluntary motion, by convulsions, or failure of reflex activity and by death.

Reflex Action.—In six experiments on frogs with the Crotalus, made in connection with a direct study of the effect on reflex action, in none of them was there found a slow, gradual diminution of reflex activity, but invariably a sudden loss of this function. The time of the occurrence of the loss of reflex activity varies very greatly. In four experiments on pithed frogs, each of the frogs was given 0.015 gram of the dried Crotalus adamanteus venom in 10 minims of distilled water, by means of injection into the posterior lymph sac. In one experiment no alteration in reflex activity occurred after one and three-quarter hours, although it seems probable that the venom was not by any means completely absorbed since the lymph sac seemed bulged with fluid which had accumulated. In another experiment no alteration occurred in one and a half hours. In a third reflex action was suddenly abolished in one hour, and in a fourth in forty-five minutes, without there being in any case gradual diminution of reflex activity preceding the complete loss.

Two experiments were made on pithed frogs to determine if the loss of reflex . activity was due to an action of the venom upon the nerves or upon the spinal cord, and for this purpose we ligated all of the bloodvessels in the right hind leg of each animal, and thus prevented the access of the venom to these parts. To each of these frogs was given 0.015 gram of the dried venom of the Crotalus adamanteus dissolved in 5 minims of distilled water, and injected into the posterior lymph sac. Reflex activity suddenly ceased in both of the frogs in one and a half hours. No reflex action was elicited by irritation of the nerves of either leg, although the motor fibres of the nerves were very excitable. We also found that direct excitation of the spinal cord in the dorsal region produced movements in the posterior extremities, but none in the anterior extremities, thus showing that impulses could travel down the cord through the motor apparatus but not upwards through the sensory portions. These observations make it clear that the loss of reflex activity is, no doubt, dependent to a great extent at least upon an action of the venom upon the sensory portions of the cord, although it is not clear that the sensory nerve fibres may not also be seriously affected.

Sensory and Motor Nerves.—In order to more directly test the action of venom upon the motor and sensory fibres we exposed the sciatic nerve along the whole extent of the thigh of pithed frogs, and placed in the middle of the exposed trunk a little (Crotalus) venom (concentrated by spontaneous evaporation). Comparative observations were now made from time to time by exciting the mixed nerve trunk above and below the point of application of the venom by means of electrodes connected with a Du Bois-Reymond induction coil, using minimum strengths of After about fifteen minutes, irritation of the foot of the leg with the poisoned nerve did not give as good reflexes as irritation of the other leg. After five hours, irritation of the trunk of the nerve below the poisoned part did not give reflexes, but above the part did give reflexes, showing that the sensory fibres were functionally destroyed by the local application of the poison. When the trunk was irritated above the poisoned part marked contraction of the muscles of the limb occurred, showing that the motor fibres and muscles were still intact. After the lapse of six hours the motor nerves would no longer respond to stimulus, although the muscles were still irritable.

From these observations it seems obvious that both the sensory and motor nerves are affected by the poison, and that the sensory nerves are far more susceptible than the motor nerves, and that the depression of the sensory nerves may be connected with the depression of reflex activity; but it seems more than likely that the loss of reflex activity is essentially of spinal origin, since there is not a slow, gradual diminution of reflex activity but a sudden paralysis—a characteristic which may be considered almost exclusively spinal.

The Spinal Cord.—We have already stated that the motor columns of the cord remain irritable after complete paralysis of the sensory columns. We have supplemented these observations by some experiments showing the direct action of venom upon the exposed spinal cord, which prove that the motor columns themselves ultimately succumb to the poison. In two experiments made upon large frogs, in which was laid bare the spinal cord in the dorsal region and in which the animals were left to fully recover from the shock, a concentrated solution of the dried venom of the Crotalus adamanteus was placed on a small portion of the cord. Before the application of the venom the cord responded actively to slight mechanical irritation; after the application of the venom there occurred a gradual impairment in irritability for the first fifteen minutes; this impairment increased, so that at the end of two hours the cord would not respond to moderate electrical stimulus. The diminution of function continued until at the end of seven hours the strongest current induced no response, although the motor nerve trunks responded actively.

Voluntary Motion.—Usually the earliest signs of nerve poisoning with venom are a disturbance of coördination and loss of voluntary motion. In frogs we found that as long as voluntary motion lasted the reflexes were active, but that with a loss of volition reflexes were at once decidedly diminished and suddenly disappeared. In frogs in which the abdominal aorta was ligated so as to prevent the poison from affecting the nerves of the posterior extremities, the results were similar.

In a number of observations made upon mammals the above conclusions were
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borne out. We have also found that the orbital reflexes are completely gone before death, and that before their loss voluntary motion disappears. Moreover, if the spinal cord is irritated immediately after the cessation of the orbital reflexes it will be found that irritation will give rise to movements in the posterior extremities only, and that after the cord will no longer respond to irritation the motor nerves are still excitable. After the motor nerves cease to respond the muscles remain irritable.

These results all go to establish the conclusion that the respiratory centre is the most vulnerable point of the nervous system, that the coördinating and volitional centres are then prominently affected, that the sensory part of the spinal cord and the sensory nerves are next attacked, and that the motor parts of the cord, and the motor nerves are the last to succumb.

#### CHAPTER VI.

# THE GLOBULINS AND PEPTONES COMPARED AS REGARDS LOCAL POISONOUS ACTIVITY.

It seems needful at this place to consider the relative local toxic capacity of globulins and peptones, the two substances found in varying quantities in all venoms as yet examined.

In order to do this effectively it will be needful at the risk of anticipating a part of what belongs strictly speaking to the pathological section, to speak briefly of the macroscopical lesions brought about at the seat of injection by these potent substances.

What takes place intensely where the injection needle enters, but represents in a violent and coarser manner lesions to be found soon or late throughout the body, and this especially applies to entire venom and to the globulins. These studies of local changes are not without definite explanatory value. It has long since been shown that the cobra and the rattlesnake are distinctive poisoners, and now our latest work seems to explain just why this is so, and enables us to see already that what might efficiently aid one bitten by the Indian serpent, would be by no means sure to succor the victim of our own less fatal snake.

Venom Peptones. Local Action.—The albuminous elements of venoms are, as already shown, two in number, and belong by virtue of their reactions respectively to the classes, peptone and globulin. Hence, as we now see with clearness, it is easy to separate them by boiling, which if brief, destroys the globulin as a poison and leaves the peptone unaltered. When after boiling we inject the fluid and coagula, we still poison, if the dose be large, for the venom peptone is toxically unchanged. The wound shows, however, hardly any of the singular appearances which characterize lesions due to fresh or unboiled venom. Boiling leaves the poison less active locally. If continued it also affects more or less the general toxicity, but this influence is most marked in the Crotaline venoms, because in them the peptone is least in amount and is also the least deadly of the two constituent poisons.

Venom Peptone.—When venom peptone in full dose is injected into the breast of a pigeon, if the animal dies within an hour or two, there is scarcely any appreciable local effect, as will be clearly seen by examining the results of experiments recorded in the chapter on the influence of various agents on the poisonous activity of venom. If the dose be smaller, so that life is prolonged, the first local effect observed is a considerable edematous swelling without any dark discoloration. After the lapse of about eighteen hours there is apt to be some discoloration, and generally a discharge of muddy putrescent serum. If the animal be killed after a

day it will be found that the muscles on the injected side about the region of the œdema are pale and bloodless, having the appearance of half-cooked chicken meat. In animals which lived longer there was sometimes found considerable congestion, marked by greenish streaks, and giving off horrible putrefactive odors. In others beneath the œdematous swelling lay a cavity about an inch in diameter, which was full of broken-down tissue, having a muddy, gangrenous appearance, and decidedly putrescent, while the surrounding muscular tissues were not apparently altered in appearance. In none of these experiments were ecchymoses found in the intestines, and in all of them the blood was coagulable.

In the following experiment Crotalus peptone obtained by dialysis was at 2:37 injected into the breast of a pigeon; 3:15 weak; 3:50 rocking slightly, no local discoloration, some slight ædematous swelling; 4:00 more unsteady on its feet; 5:45 there was considerable watery effusion in the subcutaneous cellular tissue on the side of the injection. The following afternoon there was a large swelling over the site of the wound. It was an inch or more above the healthy skin, and was apparently purely cedematous in character, there being no dark discoloration nor appearances of congestion. The superficial local effect was in every way unlike that produced by the globulins. The following afternoon (after 48 hours) the pigeon died. The swelling was unaltered as to size, and but very little discolored. The tissues around it were slightly darkened, the coloration fading away gradually at about one-half inch from the border, and there was a well-defined pale streak of tissue between the swelling and the surrounding tissue like a line of demarcation. Upon cutting into the tumor serum dropped from the incision, and the subcutaneous cellular tissue was found greatly infiltrated. The swelling seemed to be almost entirely edematous and the serum had a putrefactive odor. The muscular tissues were greatly congested and somewhat blackened, and in places as green as though infiltrated with bile. This green appearance could be seen distinctly through the skin on the surface of the superficial muscles, extending over the entire side of the breast. The odor emanating from the cut muscles was also putrefactive. In the intermuscular tissues there was some greenish gelatinous matter. Beneath the swelling was a streak of muscular tissue about one-fourth of an inch thick, which was very pale, like half-stewed meat, contrasting strongly with the other parts of the muscles.

All of these observations on slow poisoning were made with peptone derived from the venoms of the Crotalus adamanteus or the Moccasin.

Judging from the fact that the venom peptone does not give rise to any darkening of the muscular tissues within a short time after injection, and indeed, as it seems probable, not until putrefaction has set in, it is likely that the darkening and congestion which ultimately occur are to be regarded as mere secondary effects, and due to putrefactive changes induced by the poison.

The peptones, whether obtained by boiling or dialysis, seem to cause locally an enormous ædema, gradual breaking down of the tissues, and rapid production of horrible putrefactive processes, with finally a more or less extensive slough. They possess little power to produce large hemorrhages, because they do not so well as venom globulin destroy the coagulability of the blood. Hence in peptone

wounds there are only such local bleedings as are due to the leakage caused by gangrenous processes. The ragged, sodden grayish look of the muscles is very remarkable, and once seen is too unfamiliar not to be remembered as a most striking pathological appearance. For effects of peptone, see Plate I.

Venom Globulins. Local Influence.—When we inject unboiled venom, we are using globulin as well as peptone, in amounts which differ with every serpent. If we use the isolated globulins the contrast in the local phenomena as compared with those caused by peptones is immense. The different globulins already described were all examined in this connection.

As the globulins are insoluble in water free from salines, dialysis kept up long enough, as from forty-eight to seventy-two hours, in a temperature so low as to insure absence of putrefaction, will throw down the mass of the globulins in a form which enables us to collect and re-dissolve them. Three drops of Moccasin venom were mixed with 6 c. c. distilled water and dialysed by a current of pure water for fifty-six hours. As the salts passed out a precipitate increased within the dialyser. After having been washed with distilled water, it was thrown into the breast of a pigeon. Death took place in twenty-four hours. This delay in a fatal result was owing to the dose being small, and perhaps also to the fact that it did not represent all the globulin of three drops of venom; after death there was a tense black swelling at the site of the wound, and the tissues, for two inches in every direction, were soaked with black absolutely fluid blood.

It is difficult to subject venom constituents to any processes like solution or drying without more or less altering their toxicity. Desiccation certainly affects whole venom, and in a measure lessens the severity of its local symptoms. The same is true of venom globulins. An equal dose of globulin dried and redissolved takes longer to kill, than if not previously dried; also if the dried venom be given in unusual dose, the local effects are slighter than those seen with pure venom or fresh globulin in smaller dose, but killing within the same time. A long survival of course enables the local phenomena to develop and might mislead as to the fact of drying having an enfeebling influence. Desiccation greatly lessens the solubility of venom, and of its albuminous constituents, and in consequence they fail to permeate the tissues and to enter the blood at the rate which characterizes fresh venom.

In the experiment which follows, death was long delayed, and owing to this the local results were strongly marked.

A quantity of globulin obtained by dialysis, representing two grains of the venom of the *Crotalus adamanteus*, was allowed to dry. It was then placed in a little distilled water, and after a few minutes a small amount of common salt was added, which caused the venom and water to form a milky solution.

This was injected into the breast muscles of a pigeon at 3:25; 3:40 some darkening and swelling of the side of injection; 4:25 unable to stand; 6:00 convulsions, followed by death.

Autopsy.—The local effect of the venom was remarkable; beneath the skin in the arcolar tissue, over the wounded side and over half the breast of the opposite side, was a mass of bloody gelatinous effusion, and the muscles beneath on the injected

side were swollen and darkened and enormously infiltrated with blood. See Plate II., Fig. 1.

These experiments, which have been supplemented by many others, give a somewhat definite idea of the marked difference in the local effects of the globulins as a group in comparison with those produced by the boiled solution of venom, or in other words by the venom peptone.

Experiment.—The water-venom-globulin from 0.03 gram of dried venom of the Crotalus adamanteus, dissolved in a little water by means of a few crystals of salt, was injected into the breast muscles of a pigeon at 3:55. At 5:50 the animal was dead. The region of injection was terribly swollen, blackened, and suffused with liquid blood. (The amount of globulin injected was about 0.003 gram.)

In a rabbit to which had been given some of the water-venous-globulin intravenously, enormous extravasations were found when the abdominal cavity was opened.

In another experiment with the *water-venom-globulin* obtained from the venom of the Moccasin, the animal lived for some time, and very characteristic effects of slow poisoning from venom globulin were observed.

Experiment.—One c. c. of distilled water containing 0.001 gram of water-venom-globulin from the Moccasin was thrown into the breast muscles of a pigeon at 5:26. At 6:00 the local darkening and swelling of the tissues at the region of injection were noticeable. After twenty-four hours the animal was in a generally fair condition; the side was considerably darkened, and on the breast was a large swelling, which appeared to be due to a bloody effusion into the subcutaneous tissue. After forty-eight hours there was a discharge of red serum with a putrefactive odor. The whole of the side was darkened and greenish, and had the appearance of commencing gangrene.

Copper-venom-globulin.—Some of the copper-venom-globulin from the venom of the Crotalus adamanteus was injected with a little water into the breast muscles of a pigeon at 4:35. At 5:00 it was weak, but no local effects were apparent. On the following morning it was dead. The local effects were intense; there was considerable swelling, blackening, and diffusion of fluid blood. The heart was arrested midway between systole and diastole, and contained fluid blood of a dark color.

Dialysis-venom-globulin.—Some of the dialysis-venom-globulin from the venom of the Crotalus adamanteus was injected into the breast muscles of a pigeon at 5:03. At 5:18 was sickish; 5:19 unsteady, side somewhat swollen and darkened; 5:30 local effect increased. Following morning—dead. Local effects intense—great swelling, blackening, and diffusion of blood, which is incoagulable.

In another experiment, in which a larger quantity was used, the bird died in twenty-five minutes, after the occurrence of stupor, incoördination, deep laborious breathing, and convulsions. There was no time for very decided local effects, but the blood was tarry and incoagulable.

These experiments, which have been frequently repeated, render it clear that the remarkable local effects produced by the venoms of the Crotalus and Moccasin, and which are not observed after the venom is boiled, are due to the venom globulins, all of which bring about essentially the same local alterations. To fully satisfy ourselves that these interesting local effects were dependent upon the physiological activities of the globulins and not upon a possible contamination by peptone, observations were made with the *boiled* globulins. In none were there the least evidences of the presence of any poisonous element.

Whevever globulins alone are used, we have these local bleedings, fluid blood, and capillaries giving way soon after the poison reaches them. The system at large soon or late repeats the coarser phenomena of the wound; and yielding vessel walls, fluid blood, and countless hemorrhagic outflows exhibit the power of the globulins. Peptone, or, which is much the same, briefly-boiled venom, causes putrefactive changes swiftly, and shows but slight capacity to make fluid the blood, or to corrode the capillaries. The wound is foul and ædematous, but not filled with blood, whilst in its general effects the venom peptone fails again to exhibit the capacity of the globulins to multiply hemorrhages, and to destroy the natural ability of the blood by clotting to check its own wasteful expenditure.

In proportion as the peptones predominate will we have then a lessening of rapidly formed local lesions, and this is of course why Cobra venom does not give us the same terrible local consequences which ensue in *Daboia*, *Moccasin*, and *Crotalus* bites, where we have the potent combination of enough peptones and an excess of globulins. For a comparison of the local effects of Cobra and Crotalus poisoning, see Plate II., Figs. 2 and 3.

#### CHAPTER VII.

THE ACTION OF VENOMS AND THEIR ISOLATED GLOBULINS AND PEPTONES UPON THE PULSE-RATE.

#### SECTION I .- PURE VENOM.

The experiments made in connection with the pulse-rate were performed upon rabbits, and in every case, unless otherwise noted, the poison was dissolved in 1 c. c. of distilled water and injected intravenously, usually into the external jugular vein.

In researches made with the isolated poisons doses were usually employed which represented the amount of the individual poison contained in the commonly employed doses of the pure dried venom, thus giving a fair idea of the part played by the individual principles in the results produced. In some experiments, however, much larger doses were used to learn more fully the poisonous character of these substances.

In all of our observations we find that the results produced in animals, under apparently the same conditions and by using the same doses, vary very greatly; sometimes the pulse is quickened from the first and remains beyond the normal until death ensues, sometimes there is a primary diminution followed by an increase, at others there is a diminution which continues until death. The pulse is generally found to vary much in frequency. These facts all suggest that the action of the pure venom is of a complex nature; there being several factors concerned in the various alterations, and render it not improbable that in some instances ecchymoses in the various organs may account for exceptional variations.

Twenty experiments were made with pure venoms upon normal animals; six of these were made with the venom of the Crotalus adamanteus; in three the pulserate was diminished and remained below normal, in two there was a primary increase followed by a diminution, and in one of these the pulse-rate afterwards went above the normal, while in another there was a primary diminution followed by an increase. Of two experiments made with the Crotalus horridus, in one there was an increase which continued until death, and in the other an increase followed by a diminution below the normal, this diminution in turn being followed by a rise above the normal, which continued until approaching death. In two experiments with the Ancistrodon piscirorus, in one there was an increase and in the other a decrease. One experiment with the Ancistrodon contortrix gave an increase. In one experiment with the Crotalophorus miliaris there was a decrease followed by an increase. In one with the Daboia Russellii, which was not a perfectly satis-

factory experiment, there was a decrease, and in six experiments with the Cobra there was an increase in all, the increase being followed in three by a permanent decrease; in one the increase was followed by a diminution, and this in turn by an increase; in two experiments there was a permanent increase, excepting near death when a decrease ensued.

It will thus be clear that even under apparently the same conditions we cannot foretell what the alterations in the pulse-rate will be in any given experiment; although the results of the six experiments with Cobra venom are so uniform in regard to the primary increase as to indicate that with it at least we should always expect to find more or less acceleration which may or may not continue above normal, even up to the time of death.

We may also add here, that we cannot trace any relations in the alterations in the pulse, arterial pressure, and respiration to each other, so that it seems as if the changes must depend essentially upon actions peculiar to each apparatus. This holds good with the study of the pure venoms or their isolated poisons.

Action of the Pure Venoms upon the Pulse-rate in Normal Animals.

### Experiment No. 1.

		ne:	Pulsations	REMARKS.
	min.	sec.	per minute.	
Normal			285	Injected 1 drop of fresh venom from the Crotalus adamanteus
		20	285	into the thigh of a large rabbit.
		40	285	
	1	00	285	
	1	20	285	
	1	40	285	
	2	00	?	Clot in canula.
	5	0.0	285	
	7	00	285	
	. 8	0.0	285	
	9	0.0	270	
	10	0.0	270	
	11	00	240	
	12	0.0	255	
	13	0.0	270	
	20	0.0	270	
	21	30	270	
	23	. 00	270	At 1:00 the blood-pressure began falling and reached a minimum at 10:00, when it was one-third less than the normal.

#### Experiment No. 2.

	Time: min. sec	Pulsations per minute.	REMARKS.
Normal		240	Injected 3 drops of the fresh venom of the Crotalus adaman-
	20	240	teus into the thigh of a large rabbit.
	4(	240	
	1 00	195	
8	1 20 April 18		Animal broke loose and tore the canula from the artery.

13 30

13 50

14 00 16 00

16 05

16 30

17 00 300

300

280

280

water.

Repeated the injection.

Experime	ent No. 3.		
	Time:	Pulsations	REMARKS.
	min. sec.	per minute.	
Normal		255	Injected intravenously 0.003 gram dried venom of the Cro-
	10	240	talus adamanteus in 1 c. c. distilled water.
	20	225	
	30	225	
	40	210	
	50	195	
	1 00	195	
	1 20	210	
	1 40	210	
	2 00	225	
	2 20	270	
	2 40	270	
Emmanian	m + Wa 1		
Experime			
	Time: min. sec.	Pulsations per minute.	REMARKS.
Normal		300	Injected intravenously 0.003 gram dried venom of the Cro-
210121121	5	310	talus adamanteus dissolved in 1 c. c. distilled water.
	10	330	The same and the s
	20	330	·
	30	300	
	40	270	
	50	270	
	1 00	270	
	1 20	280	
	1 40	270	
	2 10	270	
	4 00	280	
	7 00	300	
	8 00	90	Struggles accompanied by remarkably slow heart beats and
	8 10	130	considerable increase of arterial pressure.
	8 20	170	•
	8 30	240	
	8 40	292	
	8 50	320	
	10 30	320	
	13 00	280	

Injected 0.003 gram dried venom dissolved in 1 c. c. distilled

Dead. Heart in complete diastole; blood incoagulable, ecchy-

moses in pericardium and peritoneum.

Exp	erimer	it No.	5.

	Time:	Pulsations	REMARKS.
	min. sec.	per minute.	
Normal		225	Injected intravenously 0.015 gram dried venom of the Cro-
	10	270	talus adamanteus dissolved in 1 c. c. distilled water.
	20	120	} Struggles.
	30	180	) Suraggies.
	40	285	
	1 00	285	
	1 20	<b>2</b> 85	
	1 40	285	
	2 00	285	
	4 00	?	Too feeble to count.
	8 00		Dead.

# Experiment No. 6.

	Tin	ne:	Pulsations	REMARKS.
	min.	sec.	per minute.	
Normal			323	Injected intravenously 0.015 gram dried venom of the Cro-
		5	315	talus adamanteus dissolved in 1 c. c. distilled water.
		20	214	
		30	225	
		40	255	
	1	00	255	
	1	30	255	
	3	30	240	
	5	30	240	
	7	30	225	
	8	00	195	
	· 13	00	195	
	17	30		Dead.

# Experiment No. 7.

	Time:	Pulsations	REMARKS.
	min. sec.	per minute.	
Normal		260	Injected intravenously 0.02 gram dried venom of the Crotalus
	5	260	adamanteus dissolved in 1 c. c. distilled water.
	20	98	Blood pressure increased, probably due to asphyxia.
	30	84	
	40	120	
	1 00		Dead.

# Experiment No. 8.

	Time:	Pulsations	REMARKS.
	min. sec.	per minute.	
Normal		300	Injected into the right carotid artery 0.015 gram dried venom
	10	195	of the Crotalus adamanteus dissolved in 1 c. c. distilled
	30	60	water.
	44	70	
	55	130	
	60	220	
	80	260	
	1 40		Dead.

# Experiment No. 9.

	Tin	ne:	Pulsations '	REMARKS.
	min.	sec.	per minute.	
Normal			225	Injected intravenously 0.015 gram dried venom of the Cro-
		10	235	talus horridus dissolved in 1 c. c. distilled water.
		20	240	
		30	240	
		50	240	
	1	00	240	
	1	10	240	
	1	20	240	
	1	30	240	
	1	40	240	
	3	40	260	
	5	40	280	
	7	40	330	*
	9	40	350	Convulsions.
	10	10		Dead.

# Experiment No. 10.

	Time	:	Pulsations	REMARKS.
	min.	sec.	per minute.	
Normal			270	Injected intravenously 0.015 gram dried venom of the Cro-
		5		talus horridus dissolved in 1 c. c. distilled water.
		10		
		20		
		30		Animal broke loose and was replaced-record before this
	2	40	370	time valueless.
	3	00	400	
	5	00	350	
	6	30	225	
	7	30	240	
	8	00	280	
	8	30	280	
	9	00	330	
	10	00	90	Respirations cease.

# Experiment No. 11.

	Time	:	Pulsations	REMARKS.
	min. s	ec.	per minute.	
Normal			216	Injected intravenously 0.004 gram dried venom of the Ancis-
	2	20	228	trodon piscivorus dissolved in 1 c. c. distilled water.
		30	228	Convulsions.
	4	40	245	
	1 .	00	252	
	1 :	30	240	Injected a similar dose.
	1 4	50	284	
	2	10	280	
	2	30	280	
	3	00	280	
	4 (	00		Killed by pithing.

# Experiment No. 12.

	Tin	ie:	Pulsations	REMARKS.
	min.	sec.	per minute.	
Normal			305	Injected intravenously 0.004 gram dried venom of the Ancis-
		10	300	trodon piscivorus dissolved in 1 c. c. distilled water.
		20	240	
		30	240	
	1	00	270	
	1	30	265	
	2	00	265	
	2	30	270	·
	3	00	275	
	5	00	300	
	5	30	300	Injected as in the foregoing.
	5	35	300	
	5	45	300	
	6	05	260	
	6	15		Convulsive movements
	6	25		S Convensive movements
	6	45	250	
	7	25	145	
	7	35	130	
	7	45	120	
	7	55	100	
	8	05	115	
	8	15	120	
	8	25	132	Animal died in a few minutes.

# Experiment No. 13.

	Tim	e:	Pulsations	REMARKS.
	min.	sec.	per minute.	
Normal			320	Injected intravenously 0.003 gram dried venom of the Ancis-
		10	320	trodon contortrix dissolved in 1 c. c. distilled water.
		30	370	
	1	00	340	
	1	30	340	
	2	00	330	
	2	30	330	
	4	30	360	
	5	30	350 -	Injected as in the foregoing.
	5	50	320	Struggles.
	6	30	250	
	6	50	360	
	7	50	390	Injection repeated.
	10	0.0		Death.

## Experiment No. 14.

1				
	Time	:	Pulsations	' REMARKS.
	min. s	sec.	per minute.	
Normal			280	Injected intravenously 0.003 gram dried venom of the Crota-
	:	20	285	lophorus miliaris dissolved in 1 c. c. distilled water.
	:	30	128	
		40	135	
		50	240	Struggles.
	1	00	285	
	1	10	285	
	2	10	290	
	2	40	300	Injected 0.006 gram.
	2	50	300	
	3	20	250	
	5	20	275	
	7	20	300	
	9	20	315	
Experime	ent No	. 15.		
	Time	:	Pulsations	REMARKS.

	Time.	1 disamons	TODATE COLOR
	min. sec.	per minute.	
Normal		240	Injected intravenously 0.003 gram dried Cobra venom dis-
	10	240	solved in 1 c. c. distilled water.
	30	250	
	1 00	260	
	1 20	250	

## Experiment No. 16.

3 20

5 20

250

260

_	Time:	Pulsations	REMARKS.
	min. sec.	per minute.	
Normal		205	Injected intravenously 0.003 gram dried Cobra venom dis-
	1 00	205	solved in 1 c. c. distilled water with a few crystals of sodie
	3 00	203	chloride.
	8 00	205	
	10 00	126	
	15 00	105	
	17 00	105	
	19 00		Dead.

Experime	ent N	o. 17.		
	Tin		Pulsations,	REMARKS.
	min.	sec.	per minute.	
Normal ,			260	Injected intravenously 0.005 gram dried Cobra venom dis-
		20	270	solved in 1 c. c. distilled water with a few crystals of sodic
		30	250	chloride.
		40	250	
	1	00	250	
	1	20	250	
	1	40	230	
	4	40	240	
	7	40	250	
	8	40	190	
	9	10		Clot in canula.
	15	00		Dead.

#### Experiment No. 18.

	Time	e:	Pulsations	REMARKS.
	min.	.958	per minute.	
Normal			310	Injected intravenously 0.015 gram dried Cobra venom dis-
		10	310	solved in 1 c. c. distilled water.
		20	320	
		30	310	
		40	260	
	1	00	310	
	1	30	330	
	2	00	340	
	2	10	340	
	6	20	150	
	6	50	150	
	7	30	165	
	8	20		Dead.

#### Experiment No. 19.

,	Time:	Pulsations	REMARKS.
	min. sec.	per minute.	
Normal		290	Injected intravenously 0.005 gram dried venom of the Daboia
	10	290	Russellii dissolved in 0.5 c. c. distilled water.
	15	280	
	20	280	
	30	280	
	40		Tetanic convulsions.
	2 00		Dead.

## Experiment No. 20.

	Tin	ne:	Pulsations	REMARKS.
	min.	sec.	per minute.	
Normai			216	Injected intravenously 0.003 gram dried venom of the Cobra
		0		dissolved in 1 c. c. distilled water.
		13		
		20	252	
		40	252	
	1	00	264	•
	1	30	288	
	2	0.0	260	
	4	0.0	264	
	9	00	231	•
	12	0.0	108	
	14	00	48	Respiration ceased; artificial respiration used.
	20		126	

Actions of Pure Venoms on the Pulse-rate in Animals with Cut Pneumogastric Nerves.—After section of the pneumogastric nerves we invariably found an increase which was, as a rule, very slight. Seven experiments in all were made on animals thus operated upon: one with the venom of the Crotalus adamanteus; one with the Crotalus horridus; one with the Ancistrodon piscivorus; one with the Ancistrodon contortrix, and three with the Cobra.

777		. 37	0.1
Hin	perime	n.t. /Vc	21.

	Time:		Pulsations	, REMARKS.
	min.	sec.	per minute.	
Normal			295	Pneumogastric nerves cut. Injected intravenously 0.003
		10	300	gram dried venom of the Crotalus adamanteus dissolved
		30	300	in 1 c. c. distilled water.
	1	00	300	
	1	30	295	·
	2	00	300	
	2	30	305	
	5	30	290	
	7	00	285	
	8	30		Injected a similar dose.
	9	30	٠	Dead.
F	7\7	. oc	)	

#### Experiment No. 22.

,		ne:	Pulsations per minute.	REMARKS.			
Normal			315	Pneumogastric nerves cut. Injected intravenously 0.00 gram dried venom of the <i>Crotalus horridus</i> dissolved 1 c. c. distilled water.			
		20		Violent struggles.			
	1	0.0	320				
	1	20	335				
	1	40	330				
	2	00	320				
	2	20	340				
	4	20	340				
	5	50	350				
	8			Dead.			

REMARKS.

# Experiment No. 23.

	min.	sec.	per minute.	
Normal			240	Pneumogastric nerves cut. Injected intravenously 0.003
		20	300	gram dried venom of the Ancistrodon piscivorus dissolved in 1 c. c. distilled water.
		30	300	Struggles.
		40	300	
		50	300	
	1	00	240	
	1	20	225	
	3	50	210	Struggles.
	5	50	270	
	6	00	300	Convulsions.
	8	00	285	
	10	00	270	
	12	00	270	
	14	00	285	
	19	0.0	240	Injected a similar dose.
	19	10	255	
	19	20	255	
	19	30	255	
	19	40	240	
	19	50	240	
	20	00	240	

Pulsations

	Tin	ne:	Pulsations	REMARKS.
	min.		per minute.	
	20	20	240	
	21	20	255	
	23	20	300	
	25	20	270	
	28	20	255	
	33	20	255	
	38	20	255	
	44	20	255	Injected a similar dose.
	44	40	225	
	45	10	• • • •	Dead.
Experime	nt N	o. 24.		
	Tin		Pulsations	REMARKS.
	min.	sec.	per minute.	
Normal			300	Pneumogastric nerves cut. Injected intravenously 0.003
		10	300	gram dried venom of the Ancistrodon contortrix dissolved
		20	310	in 1 c. c. distilled water.
		30	310	
		40	310	
	1	00	310	
	1	50	310	
	4	20	310	
	7	00	310	Injected a similar dose.
	7	05		Struggles,
	7	10	320	
	7	20	300	
	7	40	300	
	8	0.0	310	
	9	00	315	
	11	30	300	Injected a similar dose.
	11	40	295	
	12	00	290	
	12	30	290	
	13	00	290	
	13	30	290	
	19	00	285 ·	
	19	20	270	
	19	40	270	
	20	20	285	
	21	50	285	
	22	50	285	
Experime	nt N	o. 25.		•
_	Tin		Pulsations	REMARKS.
I	min.	sec.	per minute.	T
Normal		*	330	Pneumogastric nerves cut. Injected intravenously 0.003
		10	330	gram dried Cobra venom dissolved in 1 c. c. distilled water
	-	30	330	with a few crystals of sodic chloride and filtered.
	1	00	330	
	3	30	340	
	6	30	330	
	10	30	. 320	
	14	30	295	Clot formed in some
	16	30	275	Clot formed in canula.
9	may,	1886.		

Em	perime	mt A	Ja 9	26
1100	10101116	100 1	10. ~	

,1	Tin		Pulsations per minute.	' REMARKS.
Normal	1		320 315 330 330	Pneumogastric nerves cut. Injected intravenously 0.006 gram dried Cobra venom prepared as in the foregoing experiment.
	1	30	330	
	3 5	30 30	$\frac{335}{340}$	
	9	30	320	
	11 18	30 30	330	Convulsions; asphyxia; death in $2\frac{1}{2}$ minutes.

## Experiment No. 27.

1			
	Time:	Pulsations	REMARKS.
	min. sec.	per minute.	
Normal		390	Pneumogastric nerves cut. Injected intravenously 0.003
	0		gram dried Cobra venom dissolved in 1 c. c. distilled water.
	10		
	20	396	
	1 00	390	
	2 00	360	
	4 00	354	
	10		Clot in canula.
	15		Dead of asphyxia.

The Actions of Pure Venoms on Animals in which Sections of the Pneumogastric Nerves and of the Upper Cervical Portion of the Spinal Cord had been made.—After isolation of the heart from the nerve centres by making section of the pneumogastric nerves and spinal cord in the middle or upper cervical region, and maintaining the animal alive by means of artificial respiration, we find that the pulsations of the heart are almost invariably slightly diminished in frequency upon use of venom. Seven experiments were made: three with the venom of the Crotalus adamanteus; one with the Crotalus horridus; one with the Ancistrodon piscivorus; one with the Ancistrodon contortrix, and one with Cobra. In one experiment with the Crotalus adamanteus in which two doses were given, there occurred a diminution after the first dose, while there was a marked increase after the second. In the experiment with the Crotalus horridus there was but little alteration.

#### Experiment No. 28.

1	Time:	Pulsations	REMARKS.
	min. sec.	per minute.	
Normal		240	Pneumogastric nerves and cord cut. Injected intravenously
	10	235	0.003 gram dried venom of the Crotalus adamanteus dis-
	20	230	solved in 1 c. c. distilled water.
	30	225	
	40	215	
	1 00	210	
	1 20	210	
	1 40	210	
	2 40		Dead.

# Experiment No. 29.

	Time:	Pulsations	REMARKS.
	min. se	c. per minute.	
Normal		185	Pneumogastric nerves and cord cut. Injected intravenously
	1	0 185	0.003 gram dried venom of the Crotalus adamanteus dis-
	2	0 185	solved in 1 c. c. distilled water.
	36	0 180	
	1 0	0 180	
	1 2	0 180	
	3 20	180	
	3 50	180	
	5 50	160	
	7 50		Dead.

# Experiment No. 30.

	Tin	ne:	Pulsations	REMARKS.
	min.	sec.	per minute.	
Normal			240	Pneumogastric nerves and cord cut. Injected intravenously
		10	230	0.003 gram dried venom of the Crotalus adamanteus dis-
		20	230	solved in 1 c. c. distilled water.
		30	230	
		40	195	
	1	00	200	
	1	20	205	
	1	40	210	
	2	00	230	
	2	30	265	
	3	00	250	
	6	00	300?	Injected a similar dose.
	6	05	265	
	6	15		
	6	35	270	
	7	05	260	
	7	35	260	
	8	05	260	
	15	05		Dead.

# Experiment No. 31.

	Time	: Pu	lsations	REMARKS.
NT	min, s		minute.	
Normal		•	235	Pneumogastric nerves and cord cut. Injected intravenously
	]	10	230	0.015 gram dried venom of the Crotalus horridus dis-
	í	30	240	solved in 1 c. c. distilled water.
	4	10	240	
	1 (	00	235	
	2 (	00	240	
	4 (	00	240	
	6 (	00	230	
	8 (	00	220	
	12 (	00		Dead.

## Experiment No. 32.

	Tim min.		Pulsations	REMARKS.
Normal	min.		per minute. 220	Pneumogastric nerves and cord cut. Injected intravenously
		20	210	0.003 gram dried venom of the Ancistrodon piscivorus dissolved in 1 c. c. distilled water.
		30	200	Struggles.
		40	200	
	1	00	210	
	1	30	210	
	1	50	210	
	4	20	195	
	8	20	210	
	10	20	210	
	12	20	210	
	15	20	210	
	18	20	210	
	21	20	• • •	Dead.

# Experiment No. 33.

-	Tin	ne:	Pulsations	REMARKS.
	min.	sec.	per minute.	
Normal			260	Pneumogastric nerves and cord cut. Injected intravenously
		10	255	0.003 gram dried venom of the Ancistrodon contortrix
		20	250	dissolved in 1 c. c. distilled water.
		40	- 243	
	1	00	243	
	1	30	245	
	2	00	240	
	4	00	240	
	7	00	240	,
	9	00	240	
	11	00	240	
	13	00	240	
	15	00	240	
	17	0.0	240	
	20	00	240	
	22	00	240	Injected 0.006 gram.
	22	15	?	
	22	30	?	Dead.

## Experiment No. 34.

	Time:	Pulsations	REMARKS.
	min. sec	. per minute.	
Normal		220	Pneumogastric nerves and cord cut. Injected intravenously
	10	215	0.003 gram dried Cobra venom dissolved in 1 c. c. distilled
	30	215	water.
	1 00	210	
	3 00	215	
	5 00	215	
	8 00	225	
	11 00	225	
	14 00	225	
	10 00	995	Killed by pithing

Summary and Conclusions of the Actions of Venoms on the Pulse-rate.—The results of this series of experiments indicate that the primary tendency of venoms is to cause an increase of the pulse-rate, that this tendency is greater after section of the pneumogastric nerves, and that it rarely occurs after conjoined section of the pneumogastric nerves and the upper or middle cervical region of the spinal cord.

From the increased tendency to acceleration of the pulse-rate in poisoning by venom after section of the pneumogastric nerves we infer that there is some direct or indirect effect of the venom upon the pneumogastric centres by which an inhibitory influence is exerted, and which tends to neutralize the action bringing about acceleration. Since hastening of the pulse is a rare occurrence after conjoint section of the pneumogastric nerves and the cervical spinal cord, we think that the increase is due for the most part to some effect upon the accelerator centres in the medulla, whereby impulses are sent through (chiefly at least) those of the accelerator fibres which pass by the cord. The increase of the pulse-rate which may occur after division of the nerves distributed to the heart, by section of the pneumogastric nerves and cervical spinal cord, must be dependent upon a direct action of the venom upon the heart muscle or its contained ganglia.

The diminution in the heart beats must be due to a direct cardiac action, since it occurs after isolation of the heart, as above, from any central nervous influence.

In these as in all other experiments which involve intravenous use of venoms we are liable to disturbing elements which do not trouble our explanations in dealing with other poisons. At any moment, anywhere in nerve-tissue or muscles, we may have abrupt and quite countless hemorrhages. How these may introduce conflicting symptoms and modify results has already been pointed out by one of us many years ago.<sup>1</sup> They make absolute constancy of effects quite improbable.

#### SECTION II.—THE ACTIONS OF GLOBULINS ON THE PULSE-RATE,

The Actions of the Venom Globulins on the Pulse-rate.—The actions of the venom globulins upon the pulse-rate appear to differ somewhat in quality from what is found in poisoning with pure venoms; there is a greater tendency to the primary increase in the pulse than with pure venoms, while the action by which this is brought about seems to differ.

Of eleven experiments in which the amounts used represented the proportion of the respective globulins contained in the usual doses of venom given, six were made with the water-venom-globulin, two with the copper-venom-globulin, and three with the dialysis-venom-globulin; all of these poisons, excepting in one experiment with the water-venom-globulin of the Ancistrodon, were derived from the venom of the *Crotalus adamanteus*.

The water-venom-globulin seems to be the most active, and the copper-venom-

<sup>&</sup>lt;sup>1</sup> Researches on the Venom of the Rattlesnake. S. Weir Mitchell, 1861.

globulin the least so. Of the six experiments with the former, in four there was a primary increase in the pulse-rate followed by diminution, and in one case by a subsequent increase; in the other two there was a diminution from the first, the pulse regaining its normal frequency, or, as in one instance, rising above it.

In both the experiments with copper-venom-globulin there was a primary increase followed by a diminution in one case, and in the other by a return of the rate to about the normal.

In the three experiments with dialysis-venom-globulin, a primary increase occurred. In two this was followed by a drop below normal, while in the other the rate remained above the normal.

#### Experiment No. 35.

_	Time		Pulsations	73376 1 73770
	min.			REMARKS.
Normal			per minute.	Tutanta di tatan anno 1, 0,0010 anno 1, 1, 1, 1, 1
Norman			290	Injected intravenously 0.0012 gram water-venom-globulin
		10	305	(= 0.015 gram dried venom) from the venom of the Cro-
		20	310	talus adamanteus.
		40	315	
	1	00	290	
	1	30	270	
	3	00	270	
	5	00	270	
	7	00	270	
	9	00	280	
	12	00	290	
	15	00	300	
	18	00	315	
	25	00	320	
	35	00	330	
	45	00	330	
	55	00	330	Killed.

#### Experiment No. 36.

	Tim		Pulsations	REMARKS.
	min.	sec.	per minute.	
Normal		٠.	310	Injected intravenously the water-venom-globulin from 0.03
		10	310	gram dried venom of the Crotalus adamanteus.
		20	275	
		40	265	
	1	0.0	260	
	1	20	260	
	1	40	280	
	3 .	40	290	Clot in canula.
	7	40	310	
	9	40	310	Injected water-venom-globulin from 0.015 gram dried venom
	10	0.0	315	
	10	20	300	
	10	40	300	
	14	00	300	
	17	0.0	300	
	20	00	300	
	30	00	300	Killed by pithing.

Ex	periment	No.	37.
Liv,	por onecroe	2100	

<u> </u>	Time:	Pulsations per minute.	REMARKS.
Normal		320	Injected intravenously 0.0033 gram water-venom-globulin
210-1111	10	350	from the dried venom of the Crotalus adamanteus dissolved
	20	330	by the addition of a trace of sodic carbonate.
	30	305	
	50	300	
	1 10	300	
	4 10	300	Injected double dose.
	4 30	310	
	4 35	310	
	4 40	310	
	4 50	310	Injected double dose.
	15		Killed by pithing.

# Francisment No. 38

Experime	ent N	0. 38	•	
	Tim		Pulsations	REMARKS.
	min.	sec.	per minute.	
Normal			270	Injected intravenously the water-venom-globulin from one
		10	290	minim of fresh venom of the Crotalus adamanteus.
		20	295	
		30	295	
		50	260	
	1	0.0	255	
	1	30	260	
	3	30	265	
	5	30	260	
	7	30	265	
	9	30	265	
	12	30	260	
	14	30	260	
	16	30	270	
	17	30	275	
	19	30	275	
	21	30	260	Clot in canula.
	26	00	260	
	28	00	260	
	30	0.0	260	
	30	15	260	Clot in canula.
	35	0.0	260	
	37	00	260	
	39	00	255	Animal killed by pithing.

## Experiment No. 39.

1	Time:	Pulsations per minute.	REMARKS.
Normal		280	Injected intravenously the water-venom-globulin from 0.004
	30	270	gram dried venom of the Ancistrodon piscivorus dissolved
	50	230	in 1 c. c. distilled water by the addition of a few crystals of
	1 00	220 ?	sodie chloride.
	1 30	280	
	1 50	260	Injected a similar dose.
	2 00	180	
	2 40	260	
	3 10	280	

# Experiment No. 40.

	Time:		Pulsations	REMARKS.	
	min.	sec.	per minute.		
Normal			312	Injected intravenously the water-venom-globulin from 0.015	
		0		gram dried venom of the Crotalus adamanteus.	
		10	314		
		20			
		30	360		
	1	30	316		
	2	30	304		
	5	30	324		
	10	30	354		
	14	30	360	Hæmaturia.	
	19	30	396		
	24	30	384 .		
	29	30	372	†	
	34	30	372		
	42	30	372		
	47	30	372		
	52	30	372		
	57	30	360		
	67	30	316		
	77	30	316		
	80	30	120		
	85			Dead; ecchymoses in intestines; blood fluid.	

## Experiment No. 41.

Tropo, once	.,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,		
	Time min. s		
Normal		000	Injected intravenously 0.0012 gram copper-venom-globulin
	]	10 285	from the dried venom of the Crotalus adamanteus:
	5	20 290	
	é	30 285	
		50 280	
	2 :	50 270	
	4 8	50 270	
	6 5	50 260	
	8	50 260	
	10	50 255	
	11	50 260	
	17 5	20 280	
	18	20 280	Injected a similar dose.
	18	30 300	
	18	40 290	
	18	50 285	
	19	00 280	
	20	00 285	
	22	00 285	
	27	00 290	

## Experiment No. 42.

	Tim		Pulsations	REMARKS.
	min.	sec.	per minute.	
Normal		•	290	Injected intravenously 0.00225 gram copper-venom-globulin
		10	290	from the dried venom of the Crotalus adamanteus.
		30	305	
	1	00	310	
	3	00	310	
	5	00	310	
	7	00	310	
•	8	00	310	Clot in canula.
	10	0.0	310	
	12	00	312	
	22	00	280	
	24	00	280	
	26	00	280	Injected 0.0045 gram.
	26	10	285	
	26	20	290	
	26	30	290	
	27	0.0	290	
	27	00	290	
	29	00	280	·
	31	00	270	
	34	00	250	
	39	00	295	
	41	00	290	•
	43	00	285	
	45	00	285	
	52	00	295	
	58	00	295	

## Experiment No. 43.

T		•	
	Time:	Pulsations	REMARKS.
	min. seç.	per minute.	
Normal		290	Injected intravenously 0.0017 gram dialysis-venom-globulin
	20	305	from the dried venom of the Crotalus adamanteus dissolved
	40	305	in 1 c. c. distilled water with a trace of sodic carbonate.
	50	305	
	1 20	295	
	3 20	275	
	5 20	275	Animal broke loose.
	18 20	280	
	18 23		Injected 0.0034 gram dialysis-venom-globulin.
	18 30	290	
	18 45	280	
	19 05		Struggles.
	19 25	270	
	19 55	270	
	20 25	270	
	21 25	138	
	22 00	315	
	30 00		Dead.
10	May, 1886.		

#### Experiment No. 44.

	Tin		Pulsations ,	REMARKS.
	min.	sec.	per minute.	
Normal			265	Injected intravenously dialysis-venom-globulin from the dried
		20	280	venom of the Crotalus adamanteus.
		30	290	
	1	00	270	
	1	20	270	
	1	40	270	
	2	00	265	
	2	40	280	
	3	40	280	
	5	40	285	
	6	20	285	
	6	50	285	
	7	20	300	
	7	50	300	
	8	50	300	·
	9	20	300	
	9	50	300	
	10	50	300	
	11	50	300	
	12	50	300	
	14	20	300	

## Experiment No. 45.

		ne:	Pulsations per minute.	REMARKS.
Normal			270	Injected intravenously 0.0017 gram dialysis-venom-globulin
		10	280	from the dried venom of the Crotalus adamanteus.
		20	300	
		30	295	
	1	00	280	
	3	0.0	276	
	5	00	260	
	7	00	250	Clot formed in canula.
	16	00		Injected 0.0034 gram.
	17	30	255	u u u
	17	40	275	
	18	30	260	
	20	30	270	Struggles.
	23	30	260	
	28	30	260	
	43	30	270	
	53	30	290	

The Actions of the Venom Globulins on Animals with Cut Pneumogastric Nerves.—In five experiments on animals with cut pneumogastric nerves—one with the water-venom-globulin, two with copper-venom-globulin, one with dialysis-venom-globulin (all from the Crotalus adamanteus), and one with the water-venom-globulin of the Cobra—there was a tendency to a lowered pulse-rate, although in one experiment there was a primary increase, and in another a slight increase above the healthy number after repeated injections. The effects were generally less than in normal animal.

# Experiment No. 46.

-	Time:	Pulsations per minute.	REMARKS.
Normal		205	Pneumogastric nerves cut. Injected intravenously 0.0011
	10	220	gram water-venom-globulin from the dried venom of the
	20	230	Crotalus adamanteus.
	1 00	210	
	1 40	190	
	3 40	170	
	5 40	180	Clot in canula.

## Experiment No. 47.

	Tin	ie:	Pulsations	REMARKS.
	min.	sec.	per minute.	
Normal			324	Pneumogastric nerves cut. Injected intravenously water-
		0		venom-globulin from 0.035 gram dried Cobra venom dis-
		15		solved in 1 c. c. distilled water.
		25	312	
		45	318	
	1	15	264	
	2	00	300	
	4	00	304	
	8	0.0	276	
	13	00	288	
	18	00	310	
	23	0.0	319	
	28			Animal broke loose from canula.

# Experiment No. 48.

	Tin		Pulsations per minute.	REMARKS.
Normal			305 300	Pneumogastric nerves cut. Injected intravenously 0.0012 gram copper-venom-qlobulin from the dried venom of the
		40	288	Crotalus adamanteus.
	1	10	285	
	3	10	285	
	5	10	285	
	7	10	300	
	9	10	290	
	23	10	310	Injected 0.0024 gram.
	23	40	310	u u u
	24	15	310	Killed.

# Experiment No. 49.

	Time:	Pulsations	REMARKS.
	min. sec	e. per minute.	
Normal		300	Pneumogastric nerves cut. Injected intravenously 0.0012
	20	300	gram copper-venom-globulin from the dried venom of the
	40	300	Crotalus adamanteus.
	50	300	
	2 50	300	
	4 50	300	
	6 50	300	
	8 50	300	
	11 50	300	

Tin	ie:	Pulsations				REMARKS.
min.	sec.	per minute.				
13	50	300	,			
15	50	300	Injected	0.0024	gram.	
16	10	300				
16	20	300	"	44	44	
16	30	300				
16	45	300				
17	45	300	Struggle	es.		
19	45	300				
21	45	300				
23	45	270				
25	45	270				
26	45	270				
27	00	270	Animal l	killed by	y pithing.	

#### Experiment No. 50.

Lawperome					
	Time:		Pulsations	REMARKS.	
Mannal	min.	sec.	per minute.	D	
Normal			310	Pneumogastric nerves cut. Injected intravenously 0.0017	
		10	305	gram dialysis venom-globulin from the dried venom of the	
		20	300	Crotalus adamanteus.	
		30	300		
		50	310	Struggles.	
	1	50	300		
	4	20	310		
	6	20	300		
	8	20	295		
	10	20	295		
	12	20	300	Struggles.	
	17	50	300		
	18	20	300	Injected 0.0034 gram.	
	18	40	310	u = u = u	
	19	00		Struggles.	
	19	15	320	u .	
	19	20	330	u	
	21	50	320		
	23	00	310		
	25	00	310		
	27	00	310		
	29	00	310		
	34	00	305		
	34	30	300		
	38	30	290		
	41	00	280		
	47	00	217		
	49	00		Dead.	

The Actions of Venom Globulins on the Pulse-rate in Animals with the Pneumogastric Nerves and Cervical Spinal Cord Cut.—In four experiments in which the pneumogastric nerves and spinal cord in the middle cervical region were cut—one was made with the water-venom-globulin, one with the copper-venom-globulin, and two with dialysis-venom-globulin of the Crotalus adamanteus: in one experiment

there was a fall followed by a rise to the normal, and succeeded by a slight fall; in a second the pulse-rate always remained below normal, while in the third there was an almost inappreciable rise, this followed by a fall, and by an increase due to a further injection of the poison. The last showed a slight fall, then a return to the normal.

## Experiment No. 51.

	Tim	e:	Pulsations	REMARKS.
	min.	sec.	per minute.	
Normal			250	Pneumogastric nerves and cord cut. Injected intravenously
		10	250	0.0011 gram water-venom-globulin from the dried venom
		30	215	of the Crotalus adamanteus.
	1	00	240	
	1	10	240	
	2	10	245	
	3	10	245	
	5	10	245	
-	7	10	245	
	9	10	245	
	11	10	250	
	15	10	250	
	17	40	245	
	19	00	240	
	21	00	240	
	23	00	240	
	. 25	00	240	
	27	00	240	Killed.

## Experiment No. 52.

Experime	2766 IV	0. 32	/•	
	Tin	ne:	Pulsations	REMARKS.
	min.	sec.	per minute.	
Normal			255	Pneumogastric nerves and cord cut. Injected intravenously
-		10	255	0.0048 gram copper-venom-globulin from the dried venom
		20	240	of the Crotalus adamanteus.
		40	250	
	1	0.0	250	n <sub>b</sub>
	3	30	240	
	5	30	225	
	9	30	225	
	11	30	210	
	13	30	210	
	16	30	210	
	17	0.0	204	Injected 0.0048 gram.
	17	30	210	
	18	00	210	
	20	0.0	210	
	24	0.0	195	
	26	00	180	
	28	0.0	180	
	30	00	180	
	32	0.0	180	
	34	00	187	Killed.

#### Experiment No. 53.

	Time	:	Pulsations ,	REMARKS.
	min.	sec.	per minute.	
Normal			240	Pneumogastric nerves and cord cut. Injected intravenously
		10	240	0.0017 gram dialysis-venom-globulin from the dried venom
		30	245	of the Crotalus adamanteus.
	1	00	230	
	3	00	220	
	6	00	220	
	8	30	220	
	10	30	230	Injected 0.0034 gram.
	12	30	230	u u
	12	50	220	
	13	10	225	
	13	30	210	
	13	50	210	
	15	00	200	
	16	00	190	
	18	00		Dead.

### Experiment No. 54.

	Time:	Pulsations	REMARKS
	min. sec.	per minute.	
Normal		300	Pneumogastric nerves and cord cut. Injected intravenously
	10	290	0.0068 gram dialysis-venom-globulin from the dried venom
	20	290	of the Crotalus adamanteus.
	30	300	
	40	300	Tremors.
	50	300	
	1 00	300	
	1 10	300	
	1 20	300	Clot formed in canula.
	9 00		Dead.

A review of the results of these experiments with the globulins on the pulse-rate in normal animals indicates that water-venom-globulin is the most potent, and the copper-venom-globulin the least so. With the former there occurred in four of the six experiments a primary increase followed by a fall, while in the other two there was a diminution from the first. In experiments with the copper-venom-globulin and dialysis-venom-globulin there was always a primary increase, and in four out of the five experiments this was followed by a decline.

After section of the pneumogastric nerves a primary increase (due probably to some accidental cause) occurred in one out of the five experiments, in two of the other four there at first was no appreciable change, and then a diminution, while in the remaining two there was a lessening of the rate from the time of injection. These results suggest that the increase of the pulse-rate, which occurred in animals with intact vagi, was in some degree at least dependent upon an influence exerted through the pneumogastric centres and nerves. It will be observed that we here have results which are directly opposed to what we have seen with pure venom; that is a lessened tendency to the primary increase of the

pulse after section of the pneumogastric nerves. If the increase in the pulse-rate in normal animals is due for the most part to excitation of the accelerator centres, whereby impulses are generated which pass chiefly through the accelerator fibres running in the spinal cord, it would seem probable that the accelerator impulses induced by the globulins take for the most part the course of the fibres through the pneumogastric nerves, but are much feebler than the impulses which are generated by the pure venoms, and which take their path chiefly through the fibres in the spinal cord.

After section of both the pneumogastric nerves and cervical spinal cord, we found in all of our experiments a diminution in the heart-beats; this must be due to a direct action of the globulin upon the heart.

It therefore seems probable that the globulins cause a primary increase of the pulse by an excitation of the accelerator centres, whereby impulses are conveyed principally by the accelerator fibres passing through the pneumogastric nerves; and a diminution of the heart beats by a direct action on the heart.

#### SECTION III.—THE ACTIONS OF VENOM PEPTONES UPON THE PULSE-RATE

The Action of Venom Peptones on the Pulse-rate.—In seven experiments made with peptone on normal animals—four with the peptone from the venom of the Crotalus adamanteus; one with that of the Ancistrodon piscivorus; and two with that of the Cobra—we find results which vary and which resemble closely those obtained by the administration of pure venom. In three experiments there was a primary increase of pulse followed generally by a diminution; in three the pulse remained below normal; while with Ancistrodon peptone there was a primary fall of rate followed by a rise.

The differences in the results, as in previous experiments, do not seem to depend at all upon the dose or the variety of venom from which the peptone was obtained.

70		. 3	7	per per
$H_{i}$	xnerime	mt (	10.	DD.

	Time:	Pulsations	REMARKS	
27 1	min. sec	•		
Normal		280	Injected intravenously the peptone from 0.015 gram dried	
	20	102	venom of the Crotalus adamanteus.	
	30	190		
	40	190		
	50	190		
	1 00	180		
	3 00	190		
	6 00	340	Struggles.	
	11 00	285	Struggles. Broke loose.	
	49 00		Dead.	

### Experiment No. 56.

	Time: min. sec.	Pulsations , per minute.	REMARKS.
Normal		225	Injected intravenously the peptone from 0.03 gram dried
	10	260	venom of the Crotalus adamanteus.
	30	260	
	1 00	285	
	2 00	270	
	5 00	260	
	9 00	250	Killed by pithing.

### Experiment No. 57.

	Time: min. sec	Pulsations per minute.	REMARKS,
Normal		280	Injected intravenously the peptone from 0.015 gram dried
	30	280	venom of the Crotalus adamanteus.
	1 00	270	
	1 30	285	
	4 30	270	
	10 30	270	Injected double the amount.
	10 50	270	
	11 10	270	
	11 30	270	

### Experiment No. 58.

	Time:	Pulsations	REMARKS.	
	min. sec.	per minute.		
Normal		270	Injected intravenously the peptone from 0.015 gram dried	
	10	270	venom of the Crotalus adamanteus.	
	20	270		
	30	270		
	1 00	280		
	1 30	290		
	2 00	290		
	2 30	290		
	3 00	260		
	5 00	260	Injected a similar quantity.	
	5 20	260	, , , , , , , , , , , , , , , , , , ,	
	5 40	260		
	6 00	260		
	6 30	255		
	7 00	250	Injected double the quantity.	
	7 30	240		
	8 00	260		

# Experiment No. 59.

	Time:	Pulsations	REMARKS.		
	min. sec.	per minute.			
Normal		300	Injected intravenously the peptone from 0.05 gram dried		
	10	175	venom of the Ancistrodon piscivorus.		
	30	110			
	1 00	285			
	1 20	290			
	1 40	300			
	2 00	310			

Tin	Time: Pulsations			REMARKS.		X8.		
min.	sec.	per minute.						
2	20	340						
2	40	315	Injected	peptone	from	0.01	gram	venom.
5	40	340						
5	50	348						
6	00	340						
6	20	340						
6	30	340						
13	30		Killed.					

# Experiment No. 60.

		ne:	Pulsations	REMARKS,	
Normal			per minute. 225	Injected intravenously the peptone from 0.005 gram dried	
		10	220	Cobra venom.	
		20	220		
		30	220		
		40	230		
	1	00	230		
	1	20	220		
	3	20	204	Struggles.	
	6	20	165		
	11	20	280	Convulsive twitchings.	
	16	20	260		
	16	50	200		
	17	50	150		
	18	20	100	Blood is asphyxiated; no respiration.	
	18	50			
	19	00	130		
	19	10	190		
	19	30	110		
	19	50	38		
	20	10	, 35		
	20	30	35	Killed,	

### Experiment No. 61.

	Time:	Pulsations	REMARKS.
	min. sec.	per minute.	
Normal		290	Injected intravenously the peptone from 0.06 gram dried
	10	300	Cobra venom.
	15	310	
	30	240	
	50	245	
	3 20	225	
	8 20	97	Tonic convulsions.
	10 20	72	Convulsive twitchings; asphyxiated blood; respiration
	10 40	300	ceased.
	10 50	300	
	11 20	105	
	11 40	85	
	12 00	120	
	12 20	90	
11	12 40 May, 1886.		Dead.

The Actions of Venom Peptones on Animals in which the Pneumogastric Nerves had been Cut.—Four experiments were made with the peptone on animals the pneumogastric nerves of which had been previously cut. In three of the four there was a primary increase in the pulse, while in the fourth there was a temporary diminution followed by a rise above normal. These experiments are in accord with those made with pure venom, and indicate a greater tendency to primary pulse frequency after section of the pneumogastric nerves.

One of the above experiments was made with the peptone from the Crotalus adamanteus; one with the Ancistrodon piscivorus; and two with the Cobra.

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-L			
	Time:	Pulsations	REMARKS.
	min. sec	•	
Normal		285	Pneumogastric nerves cut. Injected intravenously the peptone
	10	285	from 0.015 gram dried venom of the Crotalus adamanteus.
	30	285	
	40	300	Struggles.
	50	300	
	1 00	300	
	1 20	300	
	1 30	300	
	3 30	315	
	8 30	330	Struggles.
	15 30	345	
	20 30	325	
	25 30	315	
	30 30	315	
	35 00	315	
	40 00		
	45 00		
	50 00		
	62 00		Killed.

#### Experiment No. 63.

		ne:	Pulsations per minute.	F	REMARKS.
Normal			295	Pneumogastric nerves cut.	Injected intravenously the peptone
		30	315	from 0.015 gram dried	venom of the Ancistrodon pisci-
		40	315	vorus.	*
		50	310		
	1	00	310		
	1	20	315		
	1	40	320		
	2	00	330		
	2	30	310		
	2	40	102		
	2	50	150		
	3	00	240		
	A	90		Dood	

#### Experiment No. 64.

Time:	Pulsations	REMARKS.
min. se	c. per minute.	
	230	Pneumogastric nerves cut. Injected intravenously the peptone
1	0 235	from 0.005 gram dried Cobra venom.
2	0 240	
4	0 230	
1 0	0 230	
1 3	0 230	
3 3	0 230	
5 3	0 230	
7 3	0 230	
9 3	0 220	
10 0	0 220	
21 30	0 225	Twitchings.
25 3	0 230	
26 3	0 235	Killed.
	min. se  20 40  1 00  1 3  3 3  5 3  7 30  9 30  10 00  21 30  25 30	min. sec.         per minute.            230           10         235           20         240           40         230           1         30         230           3         30         230           5         30         230           7         30         230           9         30         220           10         00         220           21         30         225           25         30         230

#### Experiment No. 65.

	Time:	Pulsations	REMARKS.
	min. sec	. per minute.	
Normal		265	Pneumogastric nerves cut. Injected intravenously the peptone
	10	265	from 0.006 gram dried Cobra venom.
	20	255	
	40	260	
	1 00	260	
	3 00	270	
	5 00	270	
	16 00	275	
	34 00		Dead.

The Actions of Venom Peptones upon the Pulse-rate of Animals after Section of the Pneumogastric Nerves and Cervical Spinal Cord.—Six experiments made on animals in which the heart was cut off from central nervous influence by section of the pneumogastric nerves and section of the spinal cord in the middle cervical region gave uniform results. Three were made with peptone from the venom of the Crotalus adamanteus; two with the peptone from the Ancistrodon piscivorus, and one with that of the Cobra. In all of these experiments there was a diminution of the pulse-rate, and usually this was well marked. These results are also in accord with what was found in experiments with pure venom.

#### Experiment No. 66.

	Time:		REMARKS.
Normal	* * * *	200	Pneumogastric nerves and cord cut. Injected intravenously
	10	185	the peptone from 0.015 gram dried venom of the Crotalus
	20	195	adamanteus.
	4(	195	1
	1 00	190	
	3 00	160	
	13 00	195	
	15 00	200	

Tin		Pulsations	REMARKS
min.	sec.	per minute.	,
17	00	190	Injected peptone from 0.03 gram dried venom.
17	30		
19	30	187	
21	30	190	
23	30	180	
25	30	170	
31	30	165	
34	30		Dead.

#### Experiment No. 67.

	Time: min. sec.	Pulsations per minute.	REMARKS.
Normal		282	Pneumogastric nerves and cord cut. Injected intravenously
	0		the peptone from 0.015 gram dried venom of the Crotalus
	15	276	adamanteus.
	20		
	30	264	
	1 00	264	
	1 30	246	
	2 00	234	

#### Experiment No. 68.

	Tin	1e:	Pulsations	REMARKS.
	min.	sec.	per minute.	
Normal			324	Pneumogastric nerves and cord cut. Injected intravenously
		0		the peptone from 0.015 gram dried Cobra venom.
		11	300	
		40	318	
	1	40	276	
	5	40	272	
	10	40	276	
	15	40	306	
	16	00		Injected a similar dasa
	16	06		Injected a similar dose.
	16	15	306	
	16	25	300	
	17	0.0	276	
	18	00	270	
	23	00		Dead

In the above series of experiments with venom peptones we find results which agree with those in which the pure venoms were used. We conclude, therefore, that the peptones cause a primary increase and a secondary diminution of the pulse-rate, and that they occasion primary hastening of the heart beat by excitation of the accelerator centres in the medulla, and that the impulses are carried through fibres passing chiefly by the spinal cord. This increase is more marked after section of the pneumogastric nerves; thus suggesting that this principle has some direct or indirect effect upon the pneumogastric centres, tending to slow the action of the heart and to neutralize the accelerator influence. Peptones cause the diminution of the heart beat by a direct action on that organ.

#### CHAPTER VIII.

# THE ACTION OF VENOMS AND THEIR ISOLATED GLOBULINS AND PEPTONES UPON THE ARTERIAL PRESSURE.

#### SECTION I.—PURE VENOM.

The experiments made on the blood pressure with venoms and their isolated poisons were all made on rabbits. The manometer tube was connected with one of the carotid arteries, and the injections were always made into the external jugular vein unless otherwise noted.

Eighteen experiments were performed with the venoms of different species of serpents, and in all of them there was a distinct lowering of the blood-pressure. It fell immediately after the injection, and indeed sometimes before injection was complete, and the fall was generally so marked as to indicate a most profound action of the poison upon some part or parts of the circulatory apparatus. If the dose be not immediately fatal the pressure gradually rises, but finally undergoes a more or less steady decline to death. At other times the pressure sinks without subsequent rise until death ensues.

The tendency in Cobra poisoning is to a decided rise of pressure following the primary fall. In five out of six experiments with this venom the primary fall was followed by a rise which went above the normal.

Of the eighteen experiments, five were made with the venom of *Crotalus adamanteus*, in two of which the poison was given hypodermatically; two with that of the *Crotalus horridus*; two with the venom of *Ancistrodon piscivorus*; one each with the poisons *Ancistrodon contortrix*, *Crotalophorus miliarius*, and *Daboia Russellii*; and six with the venom of the Cobra. In all cases ether was given freely to the animal poisoned.

Action of the Pure Venoms upon the Arterial Pressure in Normal Animals.

#### Experiment No. 1.

	Time:	Pressure	REMARKS.
37 1	min. sec.	m. m.	T
Normal		126	Injected into the thigh of a large rabbit 1 drop of fresh venom
	20	126	from the Crotalus adamanteus.
	40	126	
	1 00	124	
	1 20	122	
	1 40	120	
	2 00	118	Clot formed in canula.
	5 00	114	

1 20

1 40

2 10

58

56

54

	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
	7 00	84	,
	8 00	84	
	9 00	84	
	10 00	82	
	11 00	82	
	12 00	78	
	13 00	82	
	20 00	52	
	21 30	56	
	23 00	64	
	25 00	56	
	26	• • •	Struggles followed by death.
F			
Experime	Time:	Duoganna	REMARKS.
	min. sec.	Pressure m. m.	ALMAKAS.
Normal		144	Injected into the thigh of a rabbit 3 drops of fresh venom
	20	144	from the Crotalus adamanteus.
	40	138	
	1 00	136	
	1 20	130	
	1 40	130	
	2 00	126	Struggles. Animal tore loose from the canula.
77	1 Nr. 9		
Experime			
	Time:	Pressure	REMARKS.
Normal	min. sec.	m. m. 70	Injected intravenously 0.003 gram dried venom of the Cro-
Normai	10	58	talus adamanteus in 1 c. c. distilled water.
	20	54	tatas adamanteas in 1 c. c. distined water.
	30	60	
	40	68	
	50	68	
	1 00	68	
	1 20	68	•
	1 40	62	
	2 00	58	
	2 20	54	
	2 40	44	Death.
Experime	ent No. 4.		
Time:		Pressure	REMARKS.
	min. sec.	m.m.	
Normal		110	Injected intravenously 0.003 gram dried venom of the Cro-
	5	76	talus adamanteus dissolved in 1 c. c. distilled water.
	10	72	
	20	64	
	30	62	
	40	60	
	1 00	58	
	7 00	50	

	Time:		Pressure	REMARKS.
	min.		m. m.	
	4	00	45	
	7	00	40	
	8	00	110	Struggles.
	8	10	94	
	8	20	74	
	8	30	78	
	8	40	76	
	8	50	60	
	10	30	56	
	13	00	64	
	13	30		Injection as before.
	13	50	50	21,000,000,000,000,000,000,000,000,000,0
	14	00	50	
				w u
	16	00		
	16	05	48	
	16	30	44	
	17	00		Dead. Heart in complete diastole. Ecchymoses in pericardium and peritoneum. Blood incoagulable.
Experime	202 € <b>3</b> .7	5		
Experime	Tim		Pressure	REMARKS.
	min.		m. m.	REMARKS,
Normal			124	Injected intravenously 0.015 gram dried venom of the Cro-
210111111		10	100	talus adamanteus dissolved in 1 c. c. distilled water.
		20	60	Struggles.
			96	bit uggies.
		30		
	-	40	84	
	1	00	70	
	1	20	56	
	1	40	48	
	1	55	44	
	4	00	38	Pulse feeble.
	7	00	32	
	8	00	• • •	Dead.
Experime	nt Ne	o. 6.		
	Tin		Pressure	REMARKS.
	min.	sec.	m. m.	
Normal	•		104	Injected intravenously 0.015 gram dried venom of the Cro-
		5.	84	talus horridus dissolved in 1 c. c. distilled water
		10	68	
		20	74	
		30	80	
		40	78	
		50	70	
	1	00	64	
	1	10	60	
	1	20	56	
	1	30	52	
	1	40	48	
	3	40	40	
	5	40	44	
	7	40	46	
	9	40	42	Garantaina.
	10	10	38	Convulsions.  Dead. Some ecchymoses; blood fluid.
				Dead. Some eccuymoses; blood huid,

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_	Tim	ie:	Pressure '	REMARKS.
	min.	sec.	m. m.	
Normal			110	Injected intravenously 0.015 gram dried venom of the Cro-
		5	76	talus horridus dissolved in 1 c. c. distilled water.
		10	76	
		20	. 78	
		30	70	Animal broke loose from mouth-piece, and was firmly held
	2	40	60	and refixed.
	3	00	44	
	5	00	42	
	6	30	40	
	7	30	36	
	8	00	32	
	8	30	26	
	9	00	20	
	10	00	10	Dead. Respiration failed before the heart.

## Experiment No. 8.

	Tin	ne:	Pressure	REMARKS.
	min.	sec.	m. m.	
Normal			138	Injected intravenously 0.004 gram dried venom of the Ancis-
		20	. 80	trodon piscivorus dissolved in 1 c. c. distilled water.
		30	64	Convulsions.
		40	74	
	1	00	84	
	1	30	76	Injected as above.
	1	50	60	Struggles.
	2	10	74	
	2	30	74	
	3	0.0	84	
	4	00		Killed by pithing.

6 05

6 15

6 25

6 45

7 05

60

62

66

60

52

Experiment	ent N	o. 9.		
	Tin	ne:	Pressure	REMARKS.
	min.	sec.	m. m.	
Normal			134	Injected intravenously 0.004 gram dried venom of the Ancis-
		10	108	trodon piscivorus dissolved in 0.5 c. c. distilled water.
		20	72	
		30	70	
	2	00	70	•
	1	30	72	
	2	00	74	
	2	30	70	
	3	00	70	•
	5	00	70	
	5	30	68	Injection repeated as before
	5	35	76	·
	5	45	70	

Convulsive movements.

	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
	7 15	54	
	7 25	72	
	7 35	70	
	7 45	66	
	7 55	104	
	8 05	120	
	8 15	100	
	8 25	86	Animal died in a few minutes.
Ernevime	ent No. 10.		
Daperone	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		96	Injected intravenously 0.003 gram dried venom of the Ancis-
	10	70	trodon contortrix dissolved in 1 c. c. distilled water.
	30	76	
	1 00	72	
	1 30	72	
	2 00	72	
	2 30	70	
	4 30	48	
	5 30	48	Injection repeated.
	5 50	42	Struggles.
	6 30	50	
	6 50	50	
	7 50	46	Injection repeated.
	10 00		Dead. Heart flabby blood incoagulable; no ecchymoses.
Form out on	ent No. 11.		
Expereme	Time:	70	REMARKS.
	min. sec.	Pressure m. m.	REMARKS,
Normal		170	Injected intravenously 0.003 gram dried venom of the Crota-
	20	122	lophorus miliarius dissolved in 1 c. c. distilled water.
	อับ	120	
	30 40	120 136	
	40 50	120 136 116	
	40 50	136 116	·
	40 50 1 00	136 116 150	·
	40 50	136 116	
	40 50 1 00 1 10 2 10	136 116 150 84 108	Injection repeated as before.
	40 50 1 00 1 10 2 10 2 40	136 116 150 84 108	Injection repeated as before.
	40 50 1 00 1 10 2 10 2 40 2 50	136 116 150 84 108 106 80	Injection repeated as before.
	40 50 1 00 1 10 2 10 2 40 2 50 3 20	136 116 150 84 108 106 80 84	Injection repeated as before.
	40 50 1 00 1 10 2 10 2 40 2 50 3 20 5 20	136 116 150 84 108 106 80 84 70	Injection repeated as before.
	40 50 1 00 1 10 2 10 2 40 2 50 3 20	136 116 150 84 108 106 80 84	Injection repeated as before.  Killed by pithing.
Fann annim	40 50 1 00 1 10 2 10 2 40 2 50 3 20 5 20 7 20 9 20	136 116 150 84 108 106 80 84 70	
Experim	40 50 1 00 1 10 2 10 2 40 2 50 3 20 5 20 7 20 9 20 ent No. 12.	136 116 150 84 108 106 80 84 70 74 80	Killed by pithing.
Experime	40 50 1 00 1 10 2 10 2 40 2 50 3 20 5 20 7 20 9 20 ent No. 12.	136 116 150 84 108 106 80 84 70 74 80	
•	40 50 1 00 1 10 2 10 2 40 2 50 3 20 5 20 7 20 9 20 ent No. 12. Time: min. sec.	136 116 150 84 108 80 84 70 74 80	Killed by pithing.  REMARKS.
Experime Normal	40 50 1 00 1 10 2 10 2 40 2 50 3 20 5 20 7 20 9 20 ent No. 12. Time: min. sec.	136 116 150 84 108 80 84 70 74 80 Pressure m, m. 130	Killed by pithing.  REMARKS.  Injected intravenously 0.003 gram dried Cobra venom dis-
•	40 50 1 00 1 10 2 10 2 40 2 50 3 20 5 20 7 20 9 20 ent No. 12. Time: min. sec	136 116 150 84 108 106 80 84 70 74 80 Pressure m. m. 130 110	Killed by pithing.  REMARKS.
•	40 50 1 00 1 10 2 10 2 40 2 50 3 20 5 20 7 20 9 20  ent No. 12.  Time: min. sec 10 20	136 116 150 84 108 106 80 84 70 74 80 Pressure m, m. 130 110	Killed by pithing.  REMARKS.  Injected intravenously 0.003 gram dried Cobra venom dis-
•	40 50 1 00 1 10 2 10 2 40 2 50 3 20 5 20 7 20 9 20 20 time: min. sec 10 20 30	136 116 150 84 108 106 80 84 70 74 80 Pressure m, m. 130 110 102 96	Killed by pithing.  REMARKS.  Injected intravenously 0.003 gram dried Cobra venom dis-
•	40 50 1 00 1 10 2 10 2 40 2 50 3 20 5 20 7 20 9 20  ent No. 12.  Time: min. sec 10 20	136 116 150 84 108 106 80 84 70 74 80 Pressure m, m. 130 110	Killed by pithing.  REMARKS.  Injected intravenously 0.003 gram dried Cobra venom dis-

	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
	50	70	
	1 00	78	
	1 10	70	
	1 20	52	
	1 30	52	Convulsions.
	1 40	50	
	2 00	38	
	2 20	34	
	3 20		Dead. Heart in systole; blood clotted; no ecchymoses.
Experime	nt No. 13.		
	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		140	Injected intravenously 0.003 gram dried Cobra venom dis-
	10	150	solved in 1 c. c. distilled water.
	30	140	
	1 00	134	
	1 20	134	
	3 20	140	
	5 20	148	Death from hemorrhage; artery torn.
Eman anniona	t No. 14		
Daperine	ent No. 14.		
	Time:	Pressure	REMARKS.
Normal	min. sec.	m. m. 132	Injected introveneusly 0.002 grow dried Cohre werem die
Norman	1 00	122	Injected intravenously 0.003 gram dried Cobra venom dis- solved in 1 c. c. distilled water with a few crystals of sodic
	3 00	122	chloride.
		130	emoriae.
	10 00	138	
	15 00	106	
	17 00	66	
	18 00	48	
	19 00	• • •	Dead.
Fanerima	ent No. 15.		
	Time:	D	DESCRIPTION
	Time:	Pressure	REMARKS.
Normal	min see	m m	
	min. sec.	m. m. 145	Injected intravenously 0.003 gram dried venom of the Colors
Normai		145	Injected intravenously 0.003 gram dried venom of the Cobra dissolved in 1 c. c. distilled water
Tormar	20	$\frac{145}{142}$	Injected intravenously 0.003 gram dried venom of the Cobra dissolved in 1 c. c. distilled water.
Tvormai	20 40	145 142 135	
Totimai	20 40 1 00	145 142 135 128	
Ivormai	20 40 1 00 1 30	145 142 135 128 130	
Ivormai	20 40 1 00 1 30 2 00	145 142 135 128 130 140	
Norman	20 40 1 00 1 30 2 00 4 00	145 142 135 128 130 140	
Norman	20 40 1 00 1 30 2 00	145 142 135 128 130 140	

Respiration ceased; artificial respiration used.

158

135

14 00 20 00

### Experiment No. 16.

	Time:	Pressure	REMARKS.
	min. sec.	m. m.	*
Normal		120	Injected intravenously 0.005 gram dried Cobra venom dis-
	20	108	solved in 1 c. c. distilled water with a little sodic chloride
	30	96	and filtered.
	40	88	
	1 00	90	
	1 20	82	
	1 40	96	
	4 40	94	
	7 40	100	A clot was probably beginning to form in the canula, and no
	8 40	122	dependence is to be placed upon the after record.
	9 10	156	Struggles. Clot in canula.
	15 00		Dead.

### Experiment No. 17.

1			
	Time:	Pressure	REMARKS.
	min. see	c. m. m.	
Normal		90	Injected intravenously 0.015 gram dried Cobra venom dis-
	10	0 94	solved in 1 c. c. distilled water.
	2	0 66	
	3	0 84	
	4	0 90	
	1 0	0 88	
	1 3	0 86	
	2 0	0 78	
	2 1	0 74	
	4 1	0 90	
	4 4	0 96	
	5 1	0 92	
	6 1	0 72	
	6 2	0 60	
	6 5	0 32	
		0 24	
	8 2		Dead.

### Experiment No. 18.

	Time:	Pressure	REMARKS.
	min. sec	. m. m.	
Normal		110	Injected intravenously 0.005 gram dried venom of the Daboia
	10	112	Russellii dissolved in 0.5 c. c. distilled water,
	11		Pressure falling.
	15	80	
	20	64	
	30	46	
	40	30	Violent general convulsions.
	50	54	
	1 00	) 46	
	1 15	5 46	
	2 00	)	Dead. Heart in diastole; no ecchymoses; after twenty-four hours the blood is still fluid.

Artificial respiration was used in this experiment from the beginning.

This single experiment confirms the statements of Fayrer and of Wall in regard to the convulsivant power of Daboia. The spasms are not due to defect of oxygen, as they arise early and occur despite the use of artificial respiration. Ancistrodon venom seems to have the same capacity to produce convulsions.

The Action of Pure Venoms on the Blood Pressure of Animals with Cut Pneumogastric Nerves.—After section of the pneumogastric nerves, including the depressor fibres, we find that the same alterations occur in the blood pressure as in normal animals. Nine experiments were made altogether: two with the venom of the Crotalus adamanteus; one with the Crotalus horridus; two with the Ancistrodon piscivorus; one with the Ancistrodon contortrix; and three with the Cobra.

7.7		. 3.7	7 10	
F(x)	perimen	nt N	0.19	į

	Time: min. sec.		Pressure	REMARKS.
			m. m.	
Normal		• •	96	Injected intravenously 0.003 gram dried venom of the Cro-
		10	74	talus adamanteus dissolved in 1 c. c. distilled water.
		30	68	
	1	00	68	
	1	30	76	
	2	00	64	
	2	30	60	
	5	30	44	
	7	00	44	
	8	30	48	Injected the same as above.
	8	40	42	
	9	00	46	
	9	10	44	
	9	20	44	
	9	30	44	Dead.

#### Experiment No. 20.

	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		130	Injected intravenously 0.015 gram dried venom of the Cro-
	10	100	talus adamanteus dissolved in 1 c. c. distilled water.
	20	90	
	30	96	
	40	76	
	50	56	
	1 00	50	
	1 10	38	
	1 20	32	
	1 30	22	Dead.

### Experiment No. 21.

	Time	: Pressure	REMARKS.
	min. so	ec. m. m.	
Normal		. 144	Injected intravenously 0.015 gram dried venom of the Cro- talus horridus dissolved in 1 c. c. distilled water.
	1	0 146	Struggles.
	2	20 124	Violent struggles.
	4	10 124	
	1 0	00 94	
	1 2	20 80	
	1 4	10 70	
	2 (	00 56	
	2 2	20 54	
	4 2	20 54	
	5 5	50 44	*
	8 (	00 12	Dead.

### Experiment No. 22.

	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		90	Injected intravenously 0.0035 gram dried venom of the Ancis-
	8	76	trodon piscivorus dissolved in 1 c. c. distilled water.
	10	54	
	20	44	
	30	50	Convulsions.
	40	54	
	1 00	44	
	1 20	24	
	1 40		Dead.

### Experiment No. 23.

Experime	ent IV	0. 23	•	
	Tin		Pressure	REMARKS.
	min.	sec.	m. m.	
Normal			110	Injected intravenously 0.003 gram dried venom of the Ancis-
		10	84	trodon piscivorus dissolved in 1 c. c. distilled water.
		20	64	
		30	68	Struggles.
		40	78	
		50	76	
	1	00	72	
	1	20	66	
	3	50	52	
	5	50	64	Struggles.
	6	00	86	Convulsions.
	8	00	100	
	10	00	74	
	12	0.0	70	
	14	00	66	
	19	0.0	70	Injection repeated, using the same amount.
	19	10	70	
	19	20	52	
	19	30	98	
	19	40	68	
	.19	50	90	

#### 94 THE VENOMS OF CERTAIN THANATOPHIDE Æ.

Tin	ne:	Pressure	REMARKS.
min.	sec.	m. m. ,	
20	00	90	
20	20	72	
21	20	60	
23	20	56	
25	20	60	
28	20	70	
33	20	70	
38	20	66	
44	20	58	Third injection, same amount.
44	30	50	
44	40	48	
44	50	44	
45	00	36	
<b>4</b> 5	10	26	Dead.

### Experiment No. 24.

		ne:	Pressure	REMARKS
	min.	sec.	m. m.	
Normal			154	Injected intravenously 0.003 gram dried venom of the Ancis-
		10	114	trodon contortrix dissolved in 1 c. c. distilled water.
		20	86	
		30	76	
		40	82	
	1	00	84	
	1	50	80	
	4	20	98	
	7	00	100	Injection repeated.
	7	05	138	Struggles.
	7	10	110	
	7	20	106	
	7	40	108	
	8	00	98	
	8	30	88	
	9	0.0	80	
	11	30	78	Third injection.
	- 11	40	76	
	12	00	70	
	12	30	66	
	13	00	68	
	13	30	68	
	19	00	72	Fourth injection.
	19	20	54	
	19	40	50	
	20	20	44	
	21	50	40	
	22	50	38	Dead. Heart in diastole; blood remains fluid; muscles all respond to electrical irritation; motor nerves react feebly.

T		1 7.7.	95
$\mathbf{L}x_{l}$	periment	TAO.	20.

_	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		148	Injected intravenously 0.003 gram dried Cobra venom dis-
	10	146	solved in 1 c. c. distilled water with a few crystals of sodic
	30	136	chloride and filtered.
	1 00	140	
	1 '30	140	•
	3 30	150	
	6 30	150	
	10 30	146	
	14 30	152	
	16 30	156	Clot formed in canula. Animal killed.

### Experiment No. 26.

Daporona	2100	20.	
	Time:	Pressure	REMARKS.
	min. se	c. m. m.	
Normal		134	Injected intravenously 0.006 gram dried Cobra venom pre-
	1	0 136	pared as in the foregoing experiment.
	3	0 126	
	1 0	0 118	
	1 3	0 118	
	3 3	0 132	
	5 3	0 136	
	7 3	0 136	
	9 3	0 136	
	11 3	0 136	
	18 3	0 188	Convulsive movements; asphyxia; respiration ceased in three minutes.

#### Experiment No. 27.

Time:	Pressure	REMARKS.
min. sec.	m. m. 130	Injected intravenously 0.003 gram dried Cobra venom dis-
0		solved in 1 c. c. distilled water.
10		
20	130	
1 00	118	
2 00	118	
4 00	115	
10		Clot in canula.
15		Dead from asphyxia
	min. sec. 0 10 20 1 00 2 00 4 00 10	min. sec. m. m.  130  0  10  20 130  1 00 118  2 00 118  4 00 115  10

The Action of Pure Venoms on the Blood Pressure of Animals in which the Cervical Spinal Cord had been Divided.—Upon section of the spinal cord in the upper cervical region, by which the influence of the vaso-motor centres in the medulla is practically destroyed, the primary fall of pressure from venom is generally very slight, and after this diminution there is a secondary rise which may go above the normal. In one experiment with Crotalus adamanteus venom there was a rise of pressure for a moment at the time of injection; in one experiment with Crotalus horridus, in which a somewhat larger dose was used than in the others, there was a distinct rise of pressure a few seconds after injection, followed by a fall; and in the experiment with the Cobra the pressure never went below

the normal, but in a few moments a rise occurred which continued to increase for half an hour, when the animal was killed.

In this series we observed a marked difference from the preceding (unless the dose had been immediately toxic), since the profound primary fall of pressure was not observed, excepting in a very slight degree if at all; we found, however, that the ultimate fall of pressure still occurred, save in the case of the Cobra.

Eight experiments were made: two with Crotalus adamanteus; one with Crotalus horridus; three with Ancistrodon piscivorus; one with Ancistrodon contortrix, and one with Cobra venom.

#### Experiment No. 28.

ulfa .				
	Time	:	Pressure	REMARKS.
	min. s	ec.	m. m.	
Normal			62	Injected intravenously 0.003 gram dried venom of the Cro
		9	70	talus adamanteus dissolved in 1 c. c. distilled water.
	9	20	56	
		30	56	
	4	40	58	
	1	00	58	
	1 :	20	56	
	1 :	30	48	
	1 4	40	46	
	2	00	44	
	2	20	40	
		40	38	
		20	36	
		50	36	
	_	20	36	
		00		Dead.
	0	00	• • •	D'out.

#### Experiment No. 29.

_	Tin	ne:	Pressure	REMARKS.
	min.	sec.	m. m.	
Norma	l.		66	Injected intravenously 0.006 gram dried venom of the Cro-
		5	60	talus adamanteus dissolved in 1 c. c. distilled water.
		10	58	
		20	. 58	
		30	64	
		40	62	
		50	58	
	1	00	56	
	1	30	48	
	2	30	40	
	3	30	60	
	4	30	56	
	5	30	40	
	8	00		Dead.

THEA	CIION	) E V E I	NOMS UPON ARTERIAL PRESSURE. 97
Experim	ent No. 30.		
_	Time:	Pressure	REMARKS.
Normal	min. sec.	m. m. 30	Injected intravenously 0.015 gram dried venom of the Cro-
Mormai	20	30	talus horridus dissolved in 1 c, c. distilled water.
	40	46	tatas norradas dissorred in 1 e, e. distined water,
	ı 00	42	
	1 20	38	
	3 20	26	
	5 20	26	
	7 20	26	
	9 20	24	
	10 50	30	
	12 50	30	
	14 50	28	
	16 50	26	
	17 05	26	
	17 35	10	Conjunctival reflexes gone.
	18 00		Dead.
Experim	ent No. 31.		
rv. sm	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		56	Injected intravenously 0.007 gram dried venom of the Ancis-
	10	50	trodon piscivorus dissolved in 1 c. c. distilled water.
	20	46	
	30	46	
	40	40	
	50	34	
	1 00 3 00	$\frac{30}{22}$	
	5 00	28	
	7 00	28 26	
	10 00	18	Dead. The cord proved not to have been completely cut—a
	10 00	10	few fibres of the posterior columns remaining undivided.
Experime	ent No. 32.		
1	Time:	Pressure	REMARKS,
	min. sec.	m. m.	
Normal		58	Injected intravenously 0.003 gram dried venom of the Ancis-
	10	54	trodon piscivorus dissolved in 1 c. c. distilled water.
	20	40	
	30	32	Convulsions.
	40	26	
	50	16	Dead.
Experime	ent No. 33.		
	Time:	Pressure	REMARKS.
Normal	min. sec.	m. m.	Injected interner and 0 000 mem dailed renew of the Austr
Tormal	10	46 38	Injected intravenously 0.003 gram dried venom of the Ancis-
	20	40	trodon piscivorus dissolved in 1 c. c. distilled water.
	30	38	
	40	40	
	56	48	
	3 00	38	
	5 00	30	
	8 00	28	Dead.
13	June, 1886.	20	

#### Experiment No. 34.

1				
	Tin		Pressure	REMARKS.
	min.	sec.	m. m. ,	
Normal			52	Injected intravenously 0.003 gram dried venom of the Ancis-
		10	. 44	trodon contortrix dissolved in 1 c. c. distilled water.
		20	46	
		40	50	
	1	00	54	
	3	0.0	46	
	5	00	36	
	7	00	34	
	9	00	34	
	11	00	30	
	13	00	30	
	15	0.0	30	
	17	0.0	30	
	19	00	30	
	21	00	30	
	23	0.0	30	
	25	0.0	32	
	27	00	32	
	29	00	34	
	56	0.0	34	
	61	0.0	32	
	75	00	30	Killed by pithing.

#### Experiment No. 35.

Time:	Pressure	REMARKS.
min. sec.	m. m.	
	42	Injected intravenously 0.003 gram dried venom of the Cobra
10	. 46	dissolved in 1 c. c. distilled water with a few crystals of
30	44	sodic chloride and filtered.
1 00	42	
3 00	46	
6 00	48	
9 00	46	
12 00	50	
15 30	50	
18 30	52	
21 30	54	
24 30	56	
	54	Injected the same as the foregoing.
		Clot formed in canula. Killed animal by pithing.
	min. sec.  10 30 1 00 3 00 6 00 9 00 12 00 15 30 18 30 21 30 24 30 27 30 27 40 28 00 28 30	min. sec.         m. m.           10         46           30         44           1 00         42           3 00         46           6 00         48           9 00         46           12 00         50           15 30         50           18 30         52           21 30         54           24 30         56           27 30         54           27 40         56           28 00         64

The Action of Pure Venoms on the Blood Pressure of Animals in which the Pneumogastric, Depressor, and Sympathetic Nerves and Spinal Cord have been Severed.—Since we found in the last series of experiments that after section of the cord there did not occur such a decided primary fall of pressure, it seemed obvious that the fall of pressure must be due, in major part at least, to a toxic depression

of the vaso-motor centres. A fall of pressure does, however, ultimately occur, and, excepting in the case of the Cobra, increases until death ensues

In seven other experiments, supplementary to the above, in which we made section of the pneumogastric, depressor, and sympathetic nerves in the neck, and section of the spinal cord in the middle or upper cervical region, thus cutting off both the heart and capillaries from centric nervous influence, we obtained results which were practically the same

Three of these experiments were made with the venom of the *Crotalus adamanteus*, one with that of the *Crotalus horridus*; one with the *Ancistrodon piscivorus*; one with the *Ancistrodon contortrix*, and one with the Cobra.

#### Experiment No 36

JL.						
	Tin		Pressure	REMARKS.		
	min.	sec.	m. m.			
Normal			62	Injected intravenously 0 003 gram dried venom of the Cro-		
		10	56	talus adamanteus dissolved in 1 c c distilled water.		
		20	46			
		30	56			
		40	52			
	1	00	46			
	1	20	40			
	1	40	36			
	2	00	30			
	2	20	24	Dead. Heart arrested in diastole; blood incoagulable; a few ecchymoses in peritoneum.		
				The section of the cord was not quite complete.		

#### Experiment No. 37.

	Tin		Pressure	REMARKS.
	min.	sec.	m m.	
Normal			48	Injected intravenously 0.003 gram dried venom of the Cro-
		10	46	talus adamanteus dissolved in 1 c. c. distilled water.
		20	48	The state of the s
		30	46	
	I	0.0	48	
	1	20	46	
	3	20	40	
	3	50	32	
	5	50	36	
	7	50	30	Dead. Heart arrested in diastole; blood incoagulable; no ecchymoses in serous tissues

#### Experiment No 38.

	Time: min. sec.	Pressure m. m.	REMARKS.
Normal		30	Injected intravenously 0.003 gram dried venom of the Cro-
	5	32	talus adamanteus dissolved in 1 c. c. distilled water.
	10	28	
	20	28	
	30	26	
	40	28	
	F 0	0.0	

Experiment No. 41.

Normal

min. sec.

10

20

40

Pressure

m.m.

64

56

54

48

	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
	1 00	27 ,	
	1 30	27	
	2 00	27	
	2 30	22	
	9 30		Dead. Heart arrested in diastole; blood incoagulable, ecchymoses well-marked in peritoneum and pericardium; intestines congested; 50 c. c serum in peritoneal cavity. Section of cord complete, except anterior columns.
Experime	ent No. 39.		
	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		44	Injected intravenously 0.015 gram dried venom of the Cro-
	10	44	talus horridus dissolved in 1 c. c. distilled water.
	20	56	
	30	62	
	40	60	
	1 00	52	
	1 20 1 40	44 44	
	2 00	38	
	4 00	30	
	6 00	28	
	8 00	26	
	12 00	22	Dead.
Experime	ent No. 40.		
-	Time.	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		46	Injected intravenously 0.003 gram dried venom of the Ancis
	20	40	trodon piscivorus dissolved in 1 c. c. distilled water.
	30	48	Muscular movements.
	40	44	
	1 00	44	
	1 30	40	
	1 50	38	
	4 20	28	
	6 20	28	
	8 20	28	
	10 20	28	
	12 20	28	
	15 20	28	
	18 20 21 20	28	Dead. Blood is incoagulable; no ecchymoses in serous
	21 20	•••	membranes.

REMARKS.

Injected intravenously 0.003 gram dried venom of the Ancis-

trodon contortrix dissolved in 1 c. c. distilled water.

Tin	ie:	Pressure	REMARKS.
min.	sec.	m. m.	
1	00	42	
1	30	40	
. 2	00	42	
4	00	50	
7	00	56	
9	0.0	54	
11	00	48	
13	00	48	
15	0.0	48	
17	00	48	
20	00	48	
22	00	48	Injected 0.006 gram.
22	15	38	
22	30	32	Dead.

#### Experiment No. 42.

Zioper one			1	
	Tim	ie:	Pressure	REMARKS.
	min.	sec	m. m.	
Normal			56	Injected intravenously 0.003 gram dried venom of the Cobra
		10	60	dissolved in 1 c. c. distilled water and a few crystals of
		30	56	sodic chloride and filtered.
	1	00	52	
	3	00	48	
	5	00	48	
	8	00	52	
	11	00	58	
	14	00	60	
	19	00	62	Animal killed by pithing.

To recapitulate the actions of pure venoms upon the arterial pressure—we find that the injection of venom subcutaneously causes a progressive fall of blood pressure; when injected intravenously, there is a sudden and decided fall of pressure, which may be immediately followed by death, or by a gradual rise, to be in turn succeeded by a decline with feeble pulse as death approaches. In the Cobra there is a tendency to a rise of pressure, which may go above the normal as death appears.

After section of the pneumogastric nerves and its depressor fibres we find no alterations in the results obtained in normal animals, but when section of the cord is made in the middle or upper cervical region by which the vaso-motor centres in the medulla oblongata are practically destroyed, or when accompanying this section the nerves in the neck and the spinal cord in the middle cervical region are also cut, thus practically isolating the vaso-motor centres in the medulla and cutting off all central nervous connection with the heart, we find that the primary profound diminution of pressure is not so marked. There may even appear to be a slight tendency on the part of the arterial pressures to rise above the normal just before death. Even after section of the spinal cord, as above, we find in Cobra the increase of pressure occurring before death as in normal animals.

These results indicate that the primary positive failure of pressure is due chiefly

to a depressant action of the venom upon the vaso-motor centres in the medulla oblongata, and slightly upon the heart. The tendency to a rise of pressure, as well as the ultimate fall, must be due to some action upon the heart itself or the general systemic capillaries. It seems probable that the rise of pressure in these experiments is of capillary origin since the pulse-curves do not indicate increased heart power, and we have already had reason to believe that venom exerts a decided action upon the capillaries themselves to bring about the remarkable ecchymoses found so commonly in cases of poisoning—an instance also of peripheral irritation, applicable here, is the effect of venom on the vagi peripheries in causing an increased respiration rate. The ultimate fall of pressure seems to be cardiac in origin, since there is an accompanying diminution in the force of the beats.

#### SECTION II.—THE ACTION OF VENOM GLOBULINS UPON THE BLOOD PRESSURE.

The Action of Venom Globulins upon the Blood Pressure of Normal Animals.— Thirteen experiments were made with the globulins upon normal animals. The doses usually given were those representing the amount of globulin in 0.015 gram of dried venom. The results of all of these experiments indicate that all the globulins exert an action analogous to that of the pure venom, but that they exhibit a material difference in the relative degree of their toxicity.

Of the thirteen experiments, seven were made with the water-venom-globulin, two with the copper-venom-globulin, and four with the dialysis-venom-globulin. Of the first series, five were made with the globulin from the Crotalus adamanteus; one with that of the Ancistrodon piscivorus, and one with that of the Cobra. The second and third series were made with globulins from the Crotalus adamanteus venom.

The water-venom-globulin produces the most profound changes, causing a primary diminution of pressure almost equalling that produced by pure venom, while dialysis-venom-globulin comes next; the copper-venom-globulin has but little effect. The actions of all of these globulins is to cause a primary fall of pressure, which is followed by a rise towards the normal and more or less well marked, while if the dose is sufficiently large the rise is followed by a fall to zero at death.

In one experiment made with the globulin from 0.035 gram of dried Cobra venom there was no appreciable effect. This was probably due to the very small proportion of globulin in this variety of venom.

Ŀ	x	per	$\cdot i m$	ient	N	0. 4	£3.
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Normal 110 Injected intravenously 0.0012 gram water-venow to 10 80 (= 0.015 gram dried venom) from the dried venom)	-
•	-
10 80 (= 0.015 gram dried venom) from the dried ven	on of the
	TOTH OF THE
20 92 Crotalus adamanteus.	
40 90	
1 00 84	
1 30 84	
3 00 95	
5.00 96	
7 00 104	

# THE ACTION OF VENOMS UPON ARTERIAL PRESSURE. 103

Tin	ne:	Pressure	REMARKS.
min.	sec.	m. m.	
9	00	106	
12	00	106	
15	00	110	
18	00	116	
25	00	124	
35	0.0	130	·
45	00	130	
55	00	130	Animal killed by pithing. Heart in diastole; some ecchymoses in small intestine; blood remains fluid at the end of twenty-four hours—a few very soft clots are found.

## Experiment No. 44.

	Tin	ne:	Pressure	REMARKS.
	min.	sec.	m. m.	
Normal			130	Injected intravenously the water-venom-globulin from 0.03 gram dried venom of the Crotalus adamanteus.
		10		Pressure falling.
		20	96	
		40	96	
	1	0.0	94	
	1	20	90	
	1	40	90	
	3	40	94	
	5	40	102	Clot formed in the canula.
	7	40	108	
	9	40	108	Injected water-venom-globulin from 0.015 gram dried venom.
	10	00	104	
	10	20	104	
	10	40	104	
	14	00	106	
	17	0.0	106	
	20	00	108	
	30	00	102	Animal killed by pithing.

## Experiment No. 45.

	Time	: Pre	ssure	REMARKS.
	min. s	ec. m	. m.	
Normal		. 1:	20 Injected	ed intravenously 0.0033 gram water-venom-globulin
	1	.0	86 = 0	0.045 gram dried venom) from the dried venom of the
	2	20	96 Crote	talus adamanteus dissolved by the addition of a trace
	Ę	30	86 of so	odic carbonate.
	E	0 :	90	
	1 1	0	84	
	4	0	90 Injected	ed 0.0066 gram as in the foregoing.
	4 3	30	80	,
	4 8	35 1	04	
	4 4	10 1	00 Injected	ed a similar dose.
	4 8	50	82	
	15			by pithing. Heart arrested in diastole; few ecchyers; blood remains fluid after twenty-four hours.

### Experiment No. 46.

Experime	nt N	0. 46.		
	Tin		Pressure ·	REMARKS.
Normal	min.		m. m. 148	Injected intravenously the water-venom-globulin from one
Norman		10	120	minim of fresh venom of the Crotalus adamanteus.
		20	116	
		30	116	
		50	100	
	1	00	92	
	î	30	82	
	3	30	86	
	5	30	96	
	7	30	106	
	9	30	118	
	12	30	122	
	14	30	126	
	16	30	124	
	17	30	100	
	19	30	128	
	21	30	132	Clot in canula.
	26	00	128	
	28	00	130	
	30	00	124	
	30	15	136	Clot in canula.
	35	00	134	
	37	00	136	
	39	00	130	Animal killed by pithing; no ecchymoses; blood clots.
Experime	ent N	To. 47.		
_		me:	Pressure	REMARKS.
		sec.	m. m.	
Normal			132	Injected intravenously the water-venom-globulin from 0.004
		30	126	gram dried venom of the Ancistrodon piscivorus dissolved
		50	124	in 1 c. c. distilled water by the addition of a few crystals of
	1	00	136	sodic chloride.
	1	30	122	
	1	50	114	Injected a similar dose.
	2	00	106	
	2	40	116	
	3	10	104	
Experim	ent 1	Vo. 48	• .	
	Ti	me:	Pressure	REMARKS.
	min	sec.	m. m.	
Normal	•	• • .	115	Injected intravenously the water-venom-globulin from 0.015
		0		gram dried venom of the Crotalus adamanteus.
		10		
		20	90	•
		30	93	
	1	30	90	
	2	30	100	
	5	30	102	
	10		100	
	14	30	100	Hæmaturia.

19 30 103

### THE ACTION OF VENOMS UPON ARTERIAL PRESSURE. 105

Tin	ie:	Pressure	REMARKS.
min.	вес.	m. m.	
24	30	95	
29	30	85	
34	30	80	
42	30	75	
47	30	73	
52	30	60	
57	30	* 60	
67	30	57	
77	30	55	
80	30	38	
85			Dead; ecchymoses in intestines; blood incoagulable.

### Experiment No. 49.

	Tim	e:	Pressure	REMARKS.
	min.	sec.	m. m.	
Normal			155	Injected intravenously water-venom-globulin from 0.035 gram
		0		dried Cobra venom dissolved in 1 c. c. distilled water.
		15		
		25	158	
		45	160	
	1	15	158	
	2	0.0	157	
	4	00	153	
	8	00	153	
	13	00	153	
	18	00	143	
	23	00	153	
	28			Broke loose from canula.

## Experiment No. 50.

	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		126	Injected intravenously 0.0012 gram copper-venom-qlobulin
	10	126	(= 0.015 gram dried venom) from the dried venom of the
	20	126	Crotalus adamanteus.
	30	132	
	50	126	
	2 50	124	
	4 50	126	
	6 50	126	
	8 50	124	
	10 50	124	•
	11 50	120	
	17 20	110	
	18 20	114	Injected double the foregoing dose.
	18 30	110	
	18 40	118	
	18 50	112	
	19 00	112	
	20 00	120	
	22 00	116	
	27		Killed. Heart in systole; few ecchymoses in lungs and intes- tines; blood remains fluid after two hours.

14 June, 1886.

### Ermeniment No. 51

min.			REMARKS.
	sec.	m. m.	T
		112	Injected intravenously 0.0023 gram copper-venom-globulin
	10	114	(= 0.03 gram dried venom) from the dried venom of the
			Crotalus adamanteus.
7	00	122 .	
8	00	122	Clot in canula.
10	00	124	
12	00	118	
22	00	118	
24	00	128	
26	00	124	Injected double the dose.
26	10	124	
26	30	116	
26	40	104	
27	0.0	108	
27	30	96	
29	30	90	
31	30	98	
34	30	104	
39	00	116	
41	00	116	
43	00	116	
45	00	118	
52	00	120	
58	00	122	Killed by pithing; no ecchymoses.
	10 12 22 24 26 26 26 27 27 27 29 31 34 39 41 43 45 52 58	30 1 00 3 00 5 00 7 00 8 00 10 00 12 00 22 00 24 00 26 00 26 10 26 30 27 00 27 30 29 30 31 30 34 30 39 00 41 00 43 00 45 00 52 00	30     110       1     00     112       3     00     116       5     00     120       7     00     122       8     00     122       10     00     124       12     00     118       22     00     118       24     00     128       26     00     124       26     30     116       26     40     104       27     00     108       27     30     96       29     30     90       31     30     98       34     30     104       39     00     116       41     00     116       43     00     116       45     00     118       52     00     120       58     00     122

### Experiment No. 52.

Time: Pressure R		REMARKS.		
	min.	sec.	m. m.	
Normal			132	Injected intravenously 0.0017 gram dialysis-venom-globulin
		20	124	from the dried venom of the Crotalus adamanteus dissolved
		40	112	in 1 c. c. distilled water with a trace of sodic carbonate.
		50	116	
	1	20	108	
	3	20	108	
	5	20	120	
	18	20	130	
	18	23		Injected 0.0034 gram dialysis-venom-globulin.
	18	30	96	
	18	45	100	
	19	05	94	
	19	25	102	
	19	55	96	
	20	25	76	
	20	55	60	
	21	25	46	
	22	00	42	
	30	00		Dead. No ecchymoses; heart in diastole; blood remains fluid at the end of one hour.

18.3		, 3	T.	E 0
Lx	perime	$nt \perp$	10.	Đδ.

	Tim		Pressure	REMARKS.
	min.	sec.	m. m.	
Normal			126	Injected intravenously dialysis-venom-globulin from the dried
		20	120	venom of the Crotalus adamanteus (quantity unknown).
		30	114	
	1	00	110	
	1	20	102	
	1	40	102	
	2	0.0	100	
	2	40	- 100	
	3	40	102	
	5	40	110	
	6	20	114	•
	6	50	118	
	7	20	124	
	7	50	126	
	8	50	128	
	9	20	128	
	9	50	130	
	10	50	134	
	11	50	122	
	12	50	112	
	14	20	112	Injected more of the globulin.
	14	50	84	
	15	20	78	
	15	50	62	Killed by pithing.
	10	90	04	Eined by prining.

### Experiment No. 54.

	Tim	e:	Pressure	REMARKS.
	min.	sec.	m. m.	
Normal			150	Injected intravenously 0.0017 gram dialysis-venom-globulin
		10	118	from the dried venom of the Crotalus adamanteus.
		20	130	
		30	118	
	1	00	116	
	3	0.0	110	
	5	00	126	
	7	00	124	
	16	00	136	Injected 0.0034 gram.
	17	30	116	u u
	17	40	100	
	18	30	104	
	20	30	126	
	23	30	118	
		30	102	
		30	98	
		30	94	Animal killed.

The Action of Venom Globulins upon the Blood Pressure of Animals in which the Pneumogastric Nerves had been Severed.—Four experiments were made on animals in which the pneumogastric nerves and depressor nerves were severed. The results in these experiments do not differ in quality from those obtained in

normal animals; the effects, however, appear to be less decided than in animals with the pneumogastrics intact. Here, as in the previous experiments, the coppervenom-globulin exhibits comparatively little effect on the pressure.

Of the four experiments which were made with globulins from the *Crotalus adamanteus*, one was made with the *water-venom-globulin*; two with the *copper-venom-globulin*, and one with the *dialysis-venom-globulin*. It will be noticed that in several instances considerable rises of pressure occurred accompanied by struggles; the former effect being, no doubt, due to the latter, and not to a peculiar action of the globulin.

Experime	ent No. 55.		
	Time:	Pressure	REMARKS.
	min. sec.	m. m.	7.7.7.0
Normal		116	Injected intravenously 0.0011 gram water-venom-globulin from
	10	100	the dried venom of the Crotalus adamanteus.
	20	100	
	30	110	
	1 00	106	
	1 40	110	
	3 40	110	
	5 40	108	Clot in canula. Animal killed by pithing.
Experime	ent No. 56.		
	Time:	Pressure	REMARKS.
27 1	min. sec.	m. m.	T 1
Normal	• • • • • •	130	Injected intravenously 0.0024 gram copper-venom-globulin
	10	132	from the dried venom of the Crotalus adamanteus.
	20	132	
	30	132	
	40	132	
	1 10	132	
	3 10	132	
	5 10	128	
	7 10	128	
	9 10	128	
	23 10	136	Injected a similar dose.
	23 20	130	
	23 40	132	u u u
	23 55	132	
	24 00	116	Respiration greatly slowed.
	24 15	116	Animal broke loose. Killed by pithing.
Experime	ent No. 57.		
	Time:	Pressure	REMARKS.
27 2	min. sec.	m. m.	T : / 1 : /
Normal		116	Injected intravenously 0.0012 gram copper-venom-globulin
	20	116	from the dried venom of the Crotalus adamanteus.
	40	116	
	50	116	
	2 50	116	
	4 50	116	
	6 50	116	

8 50

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### THE ACTION OF VENOMS UPON ARTERIAL PRESSURE. 109

Tin	ne:	Pressure	REMARKS.
min.	sec.	m. m.	
11	50	116	
13	50	118	
15	50	118	Injected a double quantity.
16	10	100	
16	20	118	u u u
16	30	110	
16	45	108	
17	45	132	Struggles.
19	45	114	
21	45	112	
23	45	106	
25	45	100	
26	45	88	
27	00		Animal killed by pithing.

### Experiment No. 58.

Expereme	2166 140	. 50.		
	Time		Pressure	REMARKS.
	min. s	sec.	m. m.	T : 1.1 : 1
Normal			120	Injected intravenously 0.0017 gram dialysis-venom-globulin
		10	100	from the dried venom of the Crotalus adamanteus.
		20	112	
		30	110	
		50	150	Struggles.
		50	190	"
		20	130	
		20	120	
		20	126	
		20	122	
	12	20	120	
		50	118	
	18	20	118	Injected 0.0034 gram.
	18	30	100	
	18	40	148	Struggles. Injected a similar dose.
		00	140	u
	19	15	170	u
	19	20	176	u
	21	50	144	
	22	00	140	
	23	00	166	•
	25	00	122	
	27	00	128	
	29	00	114	Struggles.
	34	0.0	82	
	34	30	80	
	38	30	60	
	41	00	50	
	47	00	28	
	49	00		Dead.

The Action of Venom Globulins upon the Blood Pressure of Animals in which the Pneumogastric, Depressor, and Sympathetic Nerves and Cervical Spinal Cord had been Cut.—Four experiments were made on animals in which the nerves of the

neck and the cord in the middle or upper cervical region (excepting one) were cut. They were all made with the globulins from the *Crotalus adamanteus*; one with water-venom-globulin, one with copper-venom-globulin, and two with dialysis-venom-globulin.

The results of this series of experiments accord with those observed when pure venom was used, and with the preceding experiments with the globulins. The primary fall of pressure is slight, while the tendency to a secondary rise is very marked, since in three of the experiments the pressure rose above the normal. The action of water-venom-globulin on the primary fall was most marked, while in the single experiment made with copper-venom-globulin, in which eight times the quantity was given in two doses, the pressure rose slightly, and continued above normal. When the dose is sufficient to kill, the pressure ultimately gradually declines, accompanied by a feeble pulse.

In the last experiment with *dialysis-venom-globulin* it will be noticed that tremors are accompanied with a rise of pressure during their existence.

Opening .		. 3	T	FO
Hicer	erime	2mL $I$	Vn -	<u>э</u> ч.

1	Time:		Pressure
	min.	sec.	m. m.
Normal			48
		10	38
		30	38
	1	00	48
	1	10	34
	2	10	46
	3	10	42
	5	10	40
	7	10	38
	9	10	34
	11	10	30
	15	10	30
	17	40	30
	19	0.0	30
	21	00	30
	23	00	30
	25	00	30
	27	00	30

#### REMARKS.

Section of cord made below the 6th cervical vertebra. Injected intravenously 0.0011 gram water-venom-globulin from the dried venom of the Crotalus adamanteus.

Artificial respiration stopped.

Animal killed by pithing.

#### Experiment No. 60.

-			
	Tir	ne:	Pressure
	min.	sec.	m. m.
Normal			29
		10	32
		20	30
		40	32
	1	00	32
	3	30	38
	5	30	40
	. 7	30	42

#### REMARKS.

Injected intravenously 0.0048 gram copper-venom-globulin from the dried venom of the Crotalus adamanteus.

	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
	9 30	42	
	11 30	42	
	13 30	40	
	16 30	44	
	17 00	42	Injected a similar quantity.
	17 30	38	
	18 00	40	
	20 00	44	
	24 00	46	
	26 00	44	
	28 00	42	
-	30 00	40	
	32 00	40	
	34 00	40	Animal killed by pithing.
Experime	ent No. 61.		
	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		42	Injected intravenously 0.0017 gram dialysis-venom-globulin
	10	40	from the dried venom of the Crotalus adamanteus.
	30	40	
	1 00	46	
	3 00	44	
	6 00	40	
	8 30	38	
	10 30	38	
	12 30		Injected 0.0068 gram.
	12 50	44	
	13 10	48	
	13 30	46	
	13 50	48	
	15 00	36	
	16 00	46	
	18 00	28	Dead. Heart arrested in diastole; no ecchymoses; blood fluid. A few fibres of the anterior columns of the cord were uncut.
Experime	nt No. 62.		
	Time:	Pressure	REMARKS.
Normal	min. sec.	m. m.	Injected interpretable 0.0000
Normai		44	Injected intravenously 0.0068 gram dialysis-venom-globulin
	10	40	from the dried venom of the Crotalus adamanteus.
	20	40	
	30	44	TT 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
	40 50	52	Universal tremors persistent.
	1 00	62	
	1 10	62	
		60	Clat in sound
		58	Clot in canula.
	3 20	86	Blood pressure fell very low before this observation, and was
	6 50	52	raised by the tremors returning vigorously.
	6 50	22	
	8 50 9 00	8	D1 W 11 21
	9 00	• • •	Dead. No ecchymoses; blood incoagulable; heart natural.

From this series of experiments with globulins it seems clear that they possess the peculiar physiological effects of pure venoms upon the blood pressure; that the water-venom-globulin is the most powerful, and the copper-venom-globulin the least so, and that the copper-venom-globulin seems to exhibit a more marked tendency than the others to cause a rise of pressure.

#### SECTION III.—THE ACTION OF VENOM PEPTONES UPON THE BLOOD PRESSURE.

The Action of Venom Peptones upon the Blood Pressure of Normal Animals.—Seven experiments were made with the peptones from different venoms: two with that of Crotalus adamanteus; three with Ancistrodon piscivorus; and two with Cobra. The action of peptones upon the blood pressure is similar to that observed with the pure venom and the globulins, but their power to cause the primary profound fall of pressure is certainly much less, while the rise of pressure after the primary fall is decidedly more marked, and there is also a tendency to go above the normal. In two experiments, one with the peptone of the Crotalus and one with that of the Moccasin, the pressure was not primarily reduced, but there was a rise above the normal from the first. Where the animal was watched until death the pressure was observed to undergo a more or less gradual decline with feeble heartbeats. In several instances a rise of pressure was noted which was usually due to convulsive seizures.

	Ex	periment	No.	63.
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	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		140	Injected intravenously the peptone from 0.015 gram dried
	10	128	venom of the Crotalus adamanteus.
	20	128	
	30	136	
	40	128	
	50	128	
	1 00	124	
	11 00	116	
	21 00	116	Clot.
	49		Dead. No ecchymoses; lungs seem congested; blood clots readily.

#### Experiment No. 64.

Daperence	2100 110. 01.		
	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		114	Injected intravenously the peptone from 0.03 gram dried
	10	130	venom of the Crotalus adamanteus.
	30	132	
	1 00	120	
	2 00	140	
	5 00	144	
	9 00	124	Killed. Ecchymoses in the lungs; blood clots.

### THE ACTION OF VENOMS UPON ARTERIAL PRESSURE. 113

Experime	ent No. 65.		
Time:		Pressure	REMARKS.
Normal	min. sec.	m. m. 86	Injected intravenously the peptone from 0.015 gram dried
Norman	30	88	venom of the Ancistrodon piscivorus.
	1 00	88	volicia de dite en outre procesor de,
	1 30	88	
	4 30	92	
	10 30	94	Injected double the amount.
	10 50	100	
	11- 10	102	
	11 30	96	
Experime	ent No. 66.		
1	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		116	Injected intravenously the peptone from 0.015 gram dried
	10	94	venom of the Ancistrodon piscivorus.
	20	66	
	30	70	
	1 00	76	
	1 30	74	
	2 00	76	
<i>*</i>	2 30	76	
	3 00	76	Tricated a similar quantity
	5 00 5 20	66 60	Injected a similar quantity.
	5 40	66	
	6 00	68	
	6 30	66	
	7 00	62	Injected a double quantity.
	7 30	56	injected a double quantity.
	8 00	60	
Experim	ent No. 67.		
1	Time:	Pressure	REMARKS.
	min, sec.	m. m.	
Normal		140	Injected intravenously the peptone from 0.05 gram dried
	10	94	venom of the Ancistrodon piscivorus.
	20	100	Convulsions.
	30	160	46
	40	170	**
	50 1 00	190 130	ed
	1 20	130	
	1 40	142	
	2 00	136	
	2 20	136	
	2 40	136	
	5 40	118	Injected 0.005 peptone.
	5 50	114	25 Journal of the Population
	6 00	104	
	6 20	112	
	6 30	112	
	9 30	118	
	13 30	122	Killed.
15	June, 1886.		

37.3		. 31	7 00
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	Tir	ne:	Pressure	REMARKS.	
	min.	sec.	m. m.		
Normal			140	Injected intravenously the peptone from 0.005 gram dried	
		10	130	Cobra venom.	
		20	148		
		30	140		
		40	142		
	1	00	142		
	1	20	140		
	3	20,	138		
	6	20	152		
	11	20	224	Convulsive twitchings.	
	16	20	176		
	16	50	134		
	17	50	92		
	18	20	104	Blood is asphyxiated; no respiration.	
	18	50	84		
	19	00	46	•	
	19	10	46		
	19	30	38		
	19	50	36		
	20	10	40		
	20	30	40	Killed.	
-					

#### Experiment No. 69.

	Time:	Pressure	REMARKS.
	min. se	ec. m. m.	
Normal		130	Injected intravenously the peptone from 0.06 gram dried
	1	0 130	Cobra venom.
	1	5 116	
	3	0 156	
	5	0 156	
	3 2	0 140	
	8 2	0 190	Tonic convulsions.
	10 2	20 176	Convulsive twitchings; asphyxiated blood; respiration
	10 3	30 208	ceased.
	10 4	0 182	
	10 5	0 136	
	11 0	0 116	
	11 2	0 102	
	11 4	0 86	
	12 0	0 66	
	12 2	20 54	
	12 4	10 38	Dead.

The Action of Venom Peptones on the Blood Pressure of Animals with Pneumogastric and Depressor Nerves Severed .- After section of the pneumogastric and depressor nerves the results are not appreciably altered. Four experiments were made: one with Crotalus adamanteus; one with Ancistrodon piscivorus, and two with Cobra venom. In all of these experiments the pressure during the secondary rise went above the normal.

### THE ACTION OF VENOMS UPON ARTERIAL PRESSURE. 115

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Fix	perime	$nt$ IV $\epsilon$	). 10.

-	Time	: Pressure	REMARKS.
	min. se	ec. m. m.	
Normal		. 160	Injected intravenously the peptone from 0.015 gram dried
	1	.0 160	venom of the Crotalus adamanteus.
	1	5 140	
	g	30 150	·
	4	0 156	Struggles.
	5	0 156	
	1 0	0 134	
	I 2	158	
	1 8	30 164	
	3 8	30 126	
	8 8	30 122	Struggles.
	5 8	30 146	
	20 8	148	
	25 3	0 140	
	30 8	30 140	
	35 (	00 136	
	40 0	0 148	
	45 6	0 142	
	50 0	0 140	
	62 0	00 138	Killed.

## Experiment No. 71.

	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		124	Injected intravenously the peptone from 0.015 gram dried
	10	100	venom of the Ancistrodon piscivorus.
	20	140	
	30	150	
	40	130	
	50	140	
	1 00	134	
	1 20	114	
	1 · 40	116	
	2 00	136	
	2 30	124	
	2 40	110	
	2 50	124	
	3 00	136	
	3 10	110	
	3 20	96	
	4 20		Respiration ceased; heart beats.

## Experiment No. 72.

	Time:	Pressure	REMARKS.			
	min. sec.	m. m.				
Normal		138	Injected intravenously the peptone from 0.005 gram dried			
	10	142	Cobra venom.			
	20	136				
	40	134	•			
	1 00	140				
	1 20	190				

Tin	ie:	Pressure			REMARKS.
min.	sec.	m.m.			
3	30	136			
5	30	136	,		
7	30	132			
9	30	132			
10	0.0	140			
21	30	146	Twitchi	ngs.	
25	30	142			
26	30	150	Killed.	No ecchymoses.	

#### Experiment No. 73.

Daperonic	10. 10.		
	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		124	Injected intravenously the peptone from 0.006 gram dried
	10	122	Cobra venom.
	20	128	
	40	124	
	1 00	126	
	3 00	120	
	5 00	120	
	16 00	118	
	34 00		Dead. Asphyxiated; no ecchymoses; blood clots in canula.

The Action of Venom Peptones on the Blood Pressure of Animals in which the Pneumogastric, Depressor, and Sympathetic Nerves and Cervical Spinal Cord were Cut.—In five experiments on animals in which the nerves in the neck and the spinal cord in the middle or upper cervical region were cut we found that but little alteration occurred in the blood pressure until late in the poisoning, excepting in one experiment with the Ancistrodon piscivorus, in which the pressure sunk immediately and death occurred in thirty seconds. Two experiments were made with the peptone of the Crotalus adamanteus; one with the Ancistrodon piscivorus, and two with the Cobra. In all of these experiments, excepting one with Cobra, there was an immediate comparatively slight fall of pressure after injection, which was followed generally by a rise; in the excepted case of the Cobra there was a primary rise equal to 3 m. m. of mercury, which was followed by a fall, and this in turn by a rise. The pressure, as in the previous experiments, usually declines towards death.

#### Experiment No. 74.

	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		50	Injected intravenously the peptone from 0.015 gram dried
	10	50	venom of the Crotalus adamanteus.
	20	48	
	40	48	
	1 00	48	
	3 00	44	
	6 00	42	
	11 00	42	
	13 00	42	
	15 00	42	

## THE ACTION OF VENOMS UPON ARTERIAL PRESSURE. 117

Time:		Pressure	REMARKS.
	min. sec.	m. m.	T
	17 00	50	Injected the peptone from 0.03 gram dried venom.
	17 30	50	
	19 30	48	
	21 30	48	
	23 30	46	
	25 30	46	
	27 30	44	
	29 30	44	
	31 30	42	
	34 30	38	Dead. No ecchymoses; blood fluid after fifteen minutes.
Experime	ent No. 75.		
	Time:	Pressure	REMARKS.
	min. sec.	m. m.	
Normal		67	Injected intravenously the peptone from 0.015 gram dried
	15	50	venom of the Crotalus adamanteus.
	20	50	
	30	50	
	1 00	50	
	1 30	50	
	2 00	50	
Experime	ent No. 76.		
7	Time:	Pressure	REMARKS.
	min. sec.	m. m.	ALEMANIS,
Normal		50	Injected intravenously the peptone from 0.015 gram dried
	10	45	venom of the Ancistrodon piscivorus.
	18	38	<b>f</b> • • • • • • • • • • • • • • • • • • •
	30	33	
	1 00		Dead.
Experime	ent No. 77.		
	Time:	Pressure	DEVIATION
	min. sec.	m. m.	REMARKS.
Normal		128	Injected intravenously the peptone from 0.01 gram dried
	10	122	Cobra venom.
	20	132	
	30	134	
	1 00	132	
	12 00		
		138	
		136	Deal District in the second
	17 30	• • •	Dead. Blood clots readily. Ecchymoses in base of lungs.

H.m	aparama 1	one t	0 18
200	101 01100	1100 AT	o. 78.

1			*	
		ne:	Pressure	' REMARKS.
	min.	sec.	m. m.	
Normal			38	Injected intravenously the peptone from 0.015 gram dried
		11	39	Cobra venom.
		20	41	
		40	40	
	1	40	35	
	5	40	35	
	10	40	37	
	15	40	- 38	
	16	00		Training a study a day
	16	06	38	Injected a similar dose.
	16	15	38	
	16	25	43	
	16	45	43	
	17	00	43	,
	18	0.0	40	
	20	00	25	
	23	00		Dead,
	20	0.0		1 Out,

From all of the results of these experiments it seems justifiable to conclude that the isolated principles of venoms exert the poisonous actions of pure venoms on the blood pressure, and that their toxic effects are essentially simply different in degree. These various poisons all play a part in the alterations of pressure, acting towards the same end, but mainly with different degrees of intensity; the watervenom-globulin appears to be the most potent in the pressure alterations, the dialysis-venom-globulin next, then the peptone, and finally the copper-venom-globulin. The globulins are the more active in the production of the diminution of pressure, and the peptone in the secondary rise.

The globulins no doubt play a very important part in the poisonous phenomena of Crotalus poisoning, a less important part in *Ancistrodon* poisoning, and but very little in Cobra poisoning; these differences not depending as much upon differences in the quality of the globulins in the species of venom to which they belong as on differences in quantity.

#### CHAPTER IX.

## THE ACTION OF VENOMS AND THEIR ISOLATED GLOBULINS AND PEPTONES UPON RESPIRATION.

#### SECTION I .- PURE VENOM.

In our experiments on respiration rabbits were always used, and the rate of breathing was recorded on a revolving drum by the lever of a Marey's tambour, the latter being connected with the animal by means of a tracheal tube. The injections in all of the experiments, excepting two, which were subcutaneous, were made into the external jugular vein.

In experiments on normal animals we observed no qualitative difference in the several venoms used. Ten experiments were made upon normal animals: four with the venom of the *Crotalus adamanteus*; three with that of the Moccasin, *piscivorus*, and three with that of the Cobra. In eight of these experiments there was a primary increase in the respiration rate followed by a diminution far below the normal, while in two the respirations were at once diminished, and became persistently slower until death. In both of these cases death occurred very soon after injection, indicating a most profound action of the poison.

## Action of the Pure Venoms on the Respirations in Normal Animals.

277			37	- 4	
$H_{i}$ $\alpha$ :	nerim	ent .	No		

				Length of				
	Tir	ne:	Respirations	curve		REM	ARKS.	
	min.	sec.	per minute.	m.m.				
Normal			84	10	Injected	l intravenously 0.0	02 gram dri	ed venom of the
		10	180	16	Crotal	lus adamanteus d	issolved in	1 c. c. distilled
		40	84	12	water.			
	1		96					
	2	20	108					
	4	50	72	8				
	6	50	72	6				
	8	50	60	6				
	10	50	48		Convulsi	ive movements.		
	11	20	40	4	44	"		
	11	50	24	4	44	ex		
	12	20	26					
	12	50			Dead.			

	ment	

Lapor	0.,		. ~.	Length of	
	Ti	me:	Respirations	, curve	REMARKS,
	min.	sec.	per minute.	m.m.	
Normal			42	6	Injected intravenously 0.004 gram dried venom of the
		10	43	10	Crotalus adamanteus dissolved in 1 c. c. distilled water.
		40	?		Struggles, which prevent a count.
	1	00	84	12	
	2	10	30	25	Convulsive movements.
	3	40	9	23	Conjunctival reflexes gone.
	5	00	10	14	
	5	10	•••	•••	Respiration ceased. Heart still beating. The respiratory muscles respond to stimulus. The spinal cord was exposed, and the motor columns were found to respond to electrical stimulus. The motor nerves responded after the motor columns of the cord had lost their irritability.

## Experiment No. 3.

Laper	unco	00 110	. 0.	Length of	
	Tir	ne:	Respirations	curve	REMARKS.
	min.	sec.	per minute.	m.m.	
Normal			84	7	Injected intravenously 0.006 gram dried venom of the
		20	158	3	Crotalus adamanteus dissolved in 3 minims distilled
		40	120	7	water.
	1	00	96	11	
	1	30	90	10	
	2	00	96	12	
	2	30	102	10	
	3	00	120	7	Struggles.
	3	30	35	5	
	4	30	60	6	
	5	30	35	10	Conjunctival reflexes gone.
	6	30	10	7	
•	7	30	4	4	Respiration ceased. Respiratory muscles irritable.
					The spinal cord was quickly exposed; the sensory columns give no response, the motor columns are active. The motor columns of the cord fail before

## Experiment No. 4.

	Tin		Respirations per minute.	Length of curve m, m.	REMARKS.
Normal	. ·		66	6	Injected intravenously 0.015 gram dried venom of the Crotalus adamanteus dissolved in 1 c. c. distilled water.
		15			Arrest of respiration attended with a tetanic condition.
		30	36	16	
	1	0.0	12	16	
	1	50	18	6	
	2	20	?	5	
	2	25	•••		Respiration ceased. Spinal cord rapidly exposed and tested by electrical currents; sensory columns fail first then the motor columns then motor nerves.

the motor nerves.

Experiment No. 5.	Ex	nerim	ent N	o. 5.
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широг	Time		Respirations	Length of curve	REMARKS.
	min. s	ec.	per minute.	m.m.	0.11
Normal			100	9	Injected intravenously 0.004 gram dried venom of the
2,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,		10	210	8	Ancistrodon piscivorus dissolved in 5 minims dis-
	9	20	150	21	tilled water.
		30	140	20	
		40	120	23	
		50			Convulsions.
	1	10			Dead.

## Erneriment No. 6.

Exper	ımen	i IVO.	0.	Length of		
	Tim	e:	Respirations	curve		REMARKS.
	miu.	sec	per minute.	m.m.		
Normal			135	6		ravenously 0.004 gram dried venom of the don piscivorus dissolved in 1 c. c. distilled
		10	420		Struggles.	Respiration at once began to increase
		20	270	6		nd reached a maximum rapidity during the e of struggles.
		30	65	18	Tetanic mov	vements.
		40	60		££	"
		50	120	10		
	1	00	120		66	95
	1	10	60			
	1	20	90	12		
	6	20	60			
	11	20	180			
	16	20	210			
	16	30		• • •	Killed.	

## Experiment No. 7.

-				Length of	
	Tim	ie:	Respirations	curve	REMARKS.
	min.	sec.	per minute.	m.m.	
Normal			144	6	Injected intravenously 0.004 gram dried venom of the
		10	300	8	Ancistrodon piscivorus dissolved in 1 c. c. distilled
		20	240	12	water.
		30	150	11	
	5	00	60	10	
	7	00	80	7	
	12	0.0	54	7	
	18	00	70	7	
	18	05			Injected as above 0.008 gram venom.
	18	30	210	9	
	18	40	160	10	
	18	50	80	5	
	23	50	65	7	Killed by pithing.

<sup>16</sup> June, 1886.

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				Length of	
	Time	:	Respirations	' curve	REMARKS.
	min. 8	sec.	per minute.	m.m.	
Normal			60	9	Injected intravenously 0.015 gram dried Cobra venom
		20	80		dissolved in 1 c. c. distilled water and filtered.
		40	120	15	Struggles.
	1	00	100	45	tt
	1	20	60	10	
	1	40	42	38	
	2	00			Respiration ceased.

### Experiment No. 9.

1				Length of	
	Time	Re	spirations	curve	REMARKS.
	min. se	ec. pe	r minute.	m.m.	
Normal			300	8	Injected intravenously 0.015 gram dried Cobra venom
	1	0	300	9	dissolved in 1 c. c. distilled water.
	2	0	255	11	
	9	0	285	10	
	4	0	240	10	
	1 (	0	255	11	
	1 8	0	200	9	
	2 (	0	150	7	
	2 1	0	125	7	
	8 2	0			Respiration ceased.

#### Experiment No. 10.

	Tir	ne:	Respirations per minute.	REMARKS.
Normal			36	Injected intravenously 0.003 gram dried Cobra venom in solution.
		20	39	
		40	39	
	1	00	51	
	1	30	52	
	2	00	45	
	4	00	48	
	9	00	46	
	12	00	36	
	14			Respiration ceased.

The Action of Pure Venoms on the Respiration in Animals in which the Pneumogastric Nerves were Cut.—When injections are made, after section of the pneumogastric nerves, the primary increase in the respiration rate does not occur, but a diminution begins at once; and, on the whole, drops irregularly until death ensues. Four experiments were thus made: one with Crotalus adamanteus, two with Ancistrodon piscivorus, and one with Cobra venom; the results being on the whole reasonably uniform.

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_				Length of	
	Tir	ne:	Respirations	curve	REMARKS.
	min.	sec.	per minute.	m.m.	
Normal			42	7	Injected intravenously 0.002 gram dried venom of the
					Crotalus adamanteus dissolved in 1 c. c. distilled
					water.
		30	20	18	Slight struggles preceding this observation interfered
	1	00	28	10	with the marker.
	1	30	6	22	
	2	00	6	19	
	2	30	3	25	
	3	00	12	18	
	3	30	6	21	
	4	30	6	21	
	5	30	6	15	
	6	30	8	12	

## Experiment No. 12.

Liupor	UNICOMU IT	U. 1.2.		
_			Length of	•
	Time:	Respirations	curve	REMARKS.
	min. sec.	per minute.	m.m.	
Normal		103	15	Injected intravenously 0.004 gram dried venom of the
	10	94	15	Ancistrodon piscivorus dissolved in 1 c. c. distilled water.
	20	84	30	Struggles.
	30	102	25	
	40	77	25	
	50	60	28	
	1 00	60	25	
	1 10	45	30	
	1 15	• • •	• • •	Dead. Respiration ceased; heart still beats. Animal dies in tetanus.

## Experiment No. 13.

	Tin	ne:	Respirations	REMARKS.
	min.	sec.	per minute.	
Normal			102	Injected intravenously 0.003 gram dried Cobra venom dissolve
		30	57	in 1 c. c. distilled water.
	1	00	78	
	2	00	57	
	4	00	66	
	10			

## Experiment No. 14.

.*	Time:	Respirations	Length of curve	REMARKS.
	min. sec.	per minute.	m.m.	
Normal		127	17	Injected intravenously 0.004 gram dried venom of the <i>Ancistrodon piscivorus</i> dissolved in 1 c. c. distilled water.
	20	92	47	
	30	90	32	
	40	82		
	50	82		
	1 05	67		

... Respiration ceased.

In none of these experiments do we find a primary increase in the respiration rate, as in animals with intact vagi, but invariably a diminution. It seems clear, therefore, that the first result must be dependent upon an excitation of the peripheries of the pneumogastric nerves, and that the diminution of respirations is due to a centrally active cause. Should the lessened number of the respirations be central, that is, dependent upon a depression of the respiratory centres, we would expect to find that the degree of depression would depend upon the relative amount of venom coming in contact with these centres in a given space of time. We have accordingly made an experiment, in which this suggestion is admirably carried out by injecting the venom into the carotid artery, thus throwing the poison directly upon the respiratory centres.

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	Tim	ie:	Respirations	Length of curve	REMARKS.
	min.	sec.	per minute.	m.m.	· ·
Normal			78	42	Injected into the right carotid artery 0.015 gram of
		15	7	38	dried venom of Crotalus adamanteus dissolved in 1
		30	4	30	c. c. distilled water.
	1	0.0	4	25	
	1	30	10	45	Convulsions.
	2	0.0			Dead.

It seems obvious from the preceding experiments that venoms exert a double action on the respiration; first, an irritant action on the peripheries of the pneumogastric nerves, by which an increase in the respiration rate is brought about; and secondly, a depression of the respiratory centres, by which the respiration rate is diminished. Since the diminution in the respirations occurs in animals with cut pneumogastrics immediately after injection, and at a time when an increase occurs in normal animals, it is apparent that these two factors are acting in normal animals at the same time to produce opposite results; consequently, whether we have an increase or a decrease in the respirations must be dependent upon the relative degree of power exerted by one or the other of these factors. In most cases we have found a primary increase of respirations followed by a diminution; it is therefore obvious that the action of the venom upon the peripheries of the pneumogastric nerves was more than able to compensate for the depressant action of the poison upon the respiratory centres; this is very clear since no increase of respirations above normal occurs in animals with cut pneumogastrics. In the two cases in normal animals in which a decline from the first was observed, and in which the animals died in a few minutes after injection, the action of the venom upon the respiratory centres was so profound that the accelerator factor was unable to cause a rise. This is also illustrated in the experiment in which the venom was injected into the carotid artery and thrown upon the respiratory centres.

Since venom does not seem to exert other than a depressant action upon the respiratory centres, it does not appear probable that it would have an opposite effect upon the respiratory nerves, so that the effect of the venom upon the peripheries of the pneumogastric nerves is probably one of irritation rather than stimu-

lation, and probably due to some secondary cause, which is likely to be located in the profound alteration of the blood or the destructive action of the venom upon the pulmonary tissues, as illustrated, for instance, upon capillaries.

### SECTION II.—THE ACTION OF GLOBULINS ON THE RESPIRATIONS.

The Action of Venom Globulins upon the Respiration in Normal Animals.—Seven experiments were made with globulins upon normal animals: three with the water-venom-globulin of the Crotalus adamanteus; and one with the water-venom-globulin of Cobra; one with the copper-venom-globulin, and one with dialysis-venom-globulin, both from the Crotalus adamanteus.

These poisons, excepting the copper-venom-globulin, all act like the pure venoms, but generally with a less degree of intensity, causing a primary acceleration of the respiration followed by a decline. In the second experiment, however, there was no diminution, but the respirations became enormously increased so that at death they were nearly trebled in frequency. The copper-venom-globulin does not cause any primary acceleration, but simply a diminution.

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Dapor	0,,,,,,	00 210.	10.	Lonoth of		
	Tin	ne:	Respirations	Length of curve		REMARKS.
	min.		per minute.	m. m.		
Vormal			100	9	Injecte	d intravenously the water-venom-globulin from
		20	100	15	0.01	5 gram dried venom of the Crotalus adamanteus.
		40	100	12		
	1	00	96	11		
	3	0.0	96	9		
	4	00	120	10		
	5	00	120	10		
	6	0.0	132	10		•
	8	0.0	100	10		
	10	00	90	9		
	12	00	80	9		
	14	00	69	7		
	14	05			Injecte	d as above from 0.06 gram dried venom.
	14	20	80	15		
	14	40	60	10	Strugg	les.
	16	40	90	10		
	18	40	96	8		
	20	40	108	9		
	22	40	114	9		
	24	40	108	9		
	26	40	90	6		
	28	40	96	8		
	30	40	72	7		
	32	40	64	8		
	34	40	70	8		
	36	40	75	8		
	38	40	80	9		
	40	40	90	10		
	44	00	• • •	• • •	Dead.	Heart arrested in diastole; some ecchymoses.

## Experiment No. 17.

	Tin		Respirations per minute.	Length of curve m, m.	REMARKS.
Normal			75	-8	Injected intravenously 0.0158 gram water-venom-globu- lin (5 days old) from the dried venom of Crotalus adamanteus.
		15	80	8	Struggles.
		30	60		
	1	00	60		
	1	30	90		
	6	30	110		
	11	30	110		
	16	30	110		Injected the same as above.
	17	00	120		
	27	00	190		
	29	00			Dead. Blood remains fluid; some ecchymoses.

## Experiment No. 18.

	Tin	ne:	Respirations	REMARKS.
	min.	sec.	per minute.	
Normal			114	Injected intravenously the water-venom-globulin from 0.035 gram
		15		of dried Cobra venom dissolved in 1 c. c. distilled water.
		25	126	
		45	132	
	1	15	150	
	2	00	150	
	6	0.0	204	
	11	00	114	
	16	00	84	
	26	00	62	
	33	00	60	
	56	00	63	
	66	00	62	
	76	0.0	72	
	120			Killed. Animal in fair condition.

## Experiment No. 19.

				TO POST A TOTAL
		ne:	Respirations	REMARKS.
	min.	sec.	per minute.	
Normal			73	Injected intravenously the water-venom-globulin from 0.015 gram
		20	84	dried venom of the Crotalus adamanteus.
		30	78	
	1	30	120	
	2	30	108	
	5	30	96	
	10	30	96	•
	14	30.	82	Hæmaturia.
	19	30	70	
	24	30	75	
	29	30	78	
	34	30	72	
	42	30	69	
	47	30	72	
	59	50 .	9.6	

Time:		Respirations			REMARKS.
min.	sec.	per minute.			
57	30	90			
67	30	· 84			
77	30	84			
80	30	12			
85			Dead.	Ecchymoses generally;	blood fluid.

## Experiment No. 20.

Exper	ımen	t IVO.	20.	Length of	
	Tim	e:	Respirations	curve	REMARKS.
	min.		per minute.	m. m.	•
Normal			180	20	Injected intravenously the copper-venom-globulin from
		20	174	19	0.015 gram dried venom of the Crotalus adamanteus.
		40	168	19	
	1	00	168	19	
	3	30	168	20	•
	5	30	108	15	
	7	30	100	9	
	9	30	110	10	
	11	00	168	17	
	13	00	138	11	
	15	00	120	10	
	17	00	144	10	
	19	00	102	9	
	21	00	108	10	
	23	00	104	7	
	25	00	112	9	
	27	00	100	9	
	30	00	90	7	
	34	00	90	7	
	39	00	112	10	
	41	00	85	8、	
	43	00	96	7	
	45	00	108	5	
	47	00	108	7	
	49	00	76	6	
	51	00	66	7	
	53	00	80	8	
	57	00	96	8	
	59	00	90	9	
	60	00	116	10	
	63	00	118	8	
	65	00	116	10	Struggles.
	69	00	104	9	
	71	00	100	7	
	73	00	116	7	
	75	00	100	8	
	77	00	116	11	
	79	00	140	11	
	81	00	130	10	
	85	00	130	10	
	87	00	120	10	
	91	00	126	9	•
	92	00			Killed by pithing. Lungs very much ecchymosed; abdo-
	0.0				minal viscera normal; heart normal; blood coagulates.

•	24	1301	220	392	223	on	7	///	0	'/ 1
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1				Length of	
	Tir	ne:	Respirations	curve	REMARKS
	min.	sec.	per minute.	m.m.	
Normal			54	18	Injected intravenously 0.0012 gram water-venom
		10	60	16	globulin from the dried venom of the Crotalus ada
		26	54	15	manteus.
		40	54	15	
	1	0.0	48	16	
	3	00	60	17-42	Struggles.
	5	00	72	33	
	7	00	54	30	
	8	00	63	32	
	10	00	60	28	
	11	30	60	30	
	13	30	72	42	
	15	30	70	38	
	17	00	78	45	Injected 0.0022 gram water-venom-globulin.
	17	10	78	42'	
	17	20	102	38	
	18	20	72	38-78	Struggles.
	19	20	66	22	
	21	20	60	23	
	24	20	70	25	
	27	20	60	29	Injected 0.0024 gram water-venom-globulin.
	27	40	60	26	
	28	20	60	25	
	29	50			Killed by pithing; some ecchymoses.

## Experiment No. 22.

T.				Length of	
	Tin	ne:	Respirations	curve	REMARKS
	min.	sec.	per minute.	m.m.	
Normal			112	9	Injected intravenously the dialysis-venom-globulin from
		10	120	12	0.015 gram dried venom of the Crotalus adamanteus.
		20	160	16	
		30	140	16	
		40	140	15	
	1	00	140	16	
	2	00	126	10	
	5	00	156	14	
	10	00	174	15	
	12	00	130	14	
	13	30	142	10	Injected dialysis-venom-globulin from 0.06 gram of
	13	50	150	22	dried venom.
	14	30	132	13	
	19	00	130	9	
	24	00	120	8	
	29	0.0	110	10	
	39	00	80	6	
	54	00	80	3	
	55	00			Dead. Respiration ceased before the heart. Ecchy-

Dead. Respiration ceased before the heart. Ecchymoses in the lungs and in the pericardium, in the small intestine, ureters, and bladder.

The Action of Venom Globulins on the Respiration of Animals in which the Pneumogastric Nerves were Cut.—Two experiments were made on animals with cut pneumogastric nerves: one with the dialysis-venom-globulin, and one with the copper-venom-globulin, both from the Crotalus adamanteus.

In neither experiment was there an increase in the respirations; these results

being in accord with the experiments made with pure venom.

-		. 3	7	00
Expe	rimen	$t \Lambda$	0.	23.

Laper	0110010	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	~~~	Length of	
	Tin	ne:	Respirations	curve	REMARKS.
	min.	sec.	per minute.	m.m.	
Normal			42	8	Pneumogastric nerves previously cut. Injected hypo-
		10	39	10	dermically the dialysis-venom-globulin from 0.015
		20	30	12	gram dried venom of the Crotalus adamanteus.
		40	24	8	
	1	00	27	10	
	1	20	?		Struggles.
	3	20	20	9	
	5	20	35	8	
	8	20	24	5	
	18	20	30	5	
	23	20	32	6	
	36	20	42	7	Injected dialysis-venom-globulin from 0.06 gram.
	36	40	42	7	
	38	40	24	20	Struggles.
	42	00	•••		Respiration ceased; heart beats feebly; blood remains incoagulable; great ecchymoses in abdominal viscera.

#### Experiment No. 24.

Exper	imer	tt Ivo.	£4.	T 17 - C	
	Tin		Respirations	Length of	REMARKS.
	min.		per minute.	m. m.	\$6EDITIVES,
Normal	1111111	BCC.	60	5	Pneumogastric nerves previously cut. Injected intra-
240111101	•	30	54	6	venously the copper-venom-globulin from 0.015 gram
	4	00	48	5	dried venom of the Crotalus adamanteus.
	1			5	died tenom of the crossess accommons
	3	00	48		
	8	00	. 48	5	
	13	00	52	6	
	15	00	48	6	Injected copper-venom-globulin from 0.03 gram dried
	15	30	30	4	venom in two doses.
	15	40	54	15	(C) to with most impossible a broathing followed by
	16	00	?		Struggles with very irregular breathing followed by
	16	30	18	10	gasping respiration.
	19	00.	12	4	,
	24	00	20	4	
	27	00	20	5	
	30	00	30	5	
	35	00	26	5	
	39		27	5	
		00			
	41	00	30	5	
	44	00	42	6	
	49	00	30	6	Injected copper-venom-globulin from 0.12 gram dried venom in two doses.
	54	00	• • •	• • •	Respiration ceased; heart still beats; ecchymoses in heart and lungs marked.
	17	June.	1886.		

The results of these experiments with the globulins indicate that the water-renom-globulin and dialysis-venom-globulin act like the pure venom, while the copper-renom-globulin lacks the property of producing the primary acceleration of the respirations.

#### SECTION III.—THE ACTION OF VENOM PEPTONES ON THE RESPIRATION.

The Action of Venom Peptones on the Respiration in Normal Animals.—Three experiments were made on the normal animals with the venom peptones; in two with the peptone from the Crotalus adamanteus, and in one with the peptone from the Ancistrodon piscivorus. In all of these experiments the increase of the respiration rate was strongly marked.

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	Tin		Respirations	Length of curve	REMARKS.
	min.	sec.	per minute.	m. m.	
Normal			225	68	Injected intravenously the peptone from 0.03 gram
		10	255	60	dried venom of the Crotalus adamanteus obtained
		30	255	60	by boiling.
	1	00	300	56	
	2	00	270	50	
	5	00	270	50	
	9	00	270	55	Killed. Blood clots readily; moderate ecchymoses in
					the lungs

### Experiment No. 26.

_				Length of	
	Tir	ne:	Respirations	curve	REMARKS.
	min.	sec.	per minute.	m.m.	
Normal			180	11	Injected intravenously the peptone from 0.06 gram
		10	240	16	dried venom of the Ancistrodon piscivorus obtained
		30	270	15	by boiling.
		40	240		
	1	00	345		
	1	10	270		
	1	20	240		
	4	20	240		
	9	20	300		
	18	20	360	14	
	28	20	270		
	38	20	180	11	

77		. 3	T 6	214
Harm	erime	22.t. /\	(0, 2)	26.

				Length of	of
	Ti	me:	Respirations	curve	REMARKS.
	min.	sec.	per minute.	m.m.	
Normal			75	9	Injected intravenously the peptone from 0.015 gram
		10	120	42	dried venom of the Crotalus adamanteus.
	3	00	30	10	
	6	00	75	8	
	11	00	50	8	
	18	00	48	7	
	23	0.0	50	7	
	28	00	45	7	
	33	00	60	7	
	37	00	60	9	
	49				Dead. No ecchymoses; lungs slightly congested.

In one animal the increase was equal to one-third of the normal; in the second, in which a larger dose was used, the normal rate was doubled; and in the third it rose to more than one-half of the normal. There was not, however, in any of the animals that marked depression which is observed in poisoning with pure venom or venom globulins.

The Action of Venom Peptones on the Respiration in Animals in which the Pneumogastric Nerves had been previously Divided.—In one experiment in which the pneumogastric nerves were cut and in which the peptone from the venom of the Crotalus adamanteus was used, the well-marked primary increase in the respirations did not occur, there being a diminution from the first.

Experiment No. 28.

Lap	01 011601	00 110	. 20.		
				Length of	
	Time:		Respirations	curve	REMARKS.
	min.	sec.	per minute.	m.m.	
Norma	al .		80	13	Injected intravenously the peptone from 0.015 gram
		10	52	18	dried venom of the Crotalus adamanteus.
		15	37	12	
		20	25	8	
		30	22	7	
	1	00	30	8	
	1	30	30	7	
	3	30	40	9	
	8	30	60	8	Struggles.
	15	30	36	13	
	20	30	48	17	
	25	30	50	14	
	30	30	52	15	
	35	00	55	12	
	40	00	48	15	
	45	0.0	45	15	
	50	00	45	16	
	62	0.0	44	15	Killed by pithing.

In this experiment, as in those with pure venom and venom globulins in which the animals had the pneumogastrics cut, the increased respiration rate seen in normal animals did not occur. The results of the experiments with venom peptone are therefore in accord with those with the pure venom and the venom globulins.

Summary.—From the results of the observations with pure venoms and their globulins and peptones upon the respiration it seems clear that the primary action of all of the above poisons, excepting the copper-venom-globulin, is to cause an increase in the number of respirations, and secondarily to diminish the respirations below the normal. Of the different principles the peptone seems to exert the most decided power in causing the acceleration, while the copper-venom-globulin seems to utterly lack this action.

Since the primary increase of the respirations does not occur in any case after section of the pneumogastric nerves, this effect must be exerted by an action of the poisons upon the peripheries of these nerves, and since after section of these nerves a diminution of the respirations always occurs this effect must be due to a depression of the respiratory centres, as we have found that the motor nerves and muscles of respiration are irritable long after the cessation of this function.

#### CHAPTER X.

#### PATHOLOGY.

Pathology of Serpent Venoms.—The pathology of snake poisoning in man owes most of what is best in our knowledge of it to the researches of the East Indian surgeons and to American observers.

In the following observations Prof. H. F. Formad has followed with great success the lines of a research which were laid down with care by the authors of this essay. They have also been at great pains to repeat, and to verify, most of the observations made by this distinguished observer.

The Nature and Character of the Individual Morphological Constituents of Venom.—Having seen that fresh venom consists morphologically of a liquid and of a solid part, it was necessary to ascertain the exact nature and character of each.

The following means were resorted to:-

1st. The separation of the granular material (of fresh venom) by filtration and the submission to physiological tests of the liquid filtrate and of the solid residue, each separately.

2d. The exposure of fresh venom to a temperature high enough to kill organized life, and then submitting it to physiological tests.

3d. Studying the effects of venom and of its isolated morphological constituents upon dead animal substances. (Putrefaction and other experiments.)

4th. The isolation and culture of the organisms contained in venom and the testing of the physiological effects of these isolated and washed organisms (viz., of pure cultures of micrococci).

1st. Filtration Experiments with Fresh Venom.—On account of its viscid and glutinous character venom could not be satisfactorily filtered except under a high pressure through a vacuum filter. About two drachms of fresh Crotalus adamanteus venom were forced by means of a hydraulic air pump through a porous clay cylinder such as is employed in certain small galvanic batteries, or else the venom was filtered through a thin layer of plaster of Paris moulded in the neck of a small glass filter. The liquid filtrate obtained was perfectly clear, and examined under the microscope showed no organic or solid particles of any kind. The solid residue left upon the filter consisted of granular material, such as has been described before, of bacteria and a few cells. This residue was diligently and repeatedly washed with boiled distilled water, by passing the latter through the filter.

The amount of residue (about three grains) just obtained was dried and introduced subcutaneously into the pectoral muscle of a pigeon, but without effect. Two pigeons were injected in the pectoral muscle, one with five, and the other with two minims of the liquid filtrate above described, and both died promptly within six minutes and twenty-five minutes respectively.

2d. Experiments with Heated Venom.—Fresh Crotalus venom rapidly dried was put in a covered watch-glass and subjected for one hour to a temperature of 115° C. in the dry-heat oven. The venom was thereby converted into a dense resinous opaque brown mass.

Two grains of this mass, upon the addition of distilled water forming a turbid liquid, were divided into thirds and injected hypodermatically into a rabbit, a rat, and a pigeon, respectively. The rabbit died in 15 minutes, the rat in 12 minutes, and the pigeon in 7 minutes, after the operation, with results and lesion similar to those obtained by the use of fresh venom.

This experiment also shows that the virulence of venom does not reside in any of its organized constituents.

3d. Putrefaction Experiments.—The testing of the effects of venom on various dead animal substances was particularly desirable on account of the remarkable capacity of the venom to induce rapid putrefaction in the tissues of living animals. It was necessary to learn whether this property of bringing about speedy necrotic changes was an action inherent in venom or due to any of its accidental constituents.

Putrefaction Experiments with Sterilized Bouillon and Fresh Venom and its Active Principles (not Sterilized).—This bouillon was prepared from chicken in the same manner as that ordinarily used for culture liquids for bacteria, and the experiments were executed in a room at a temperature of about 70° F.

About two drachms of sterilized bouillon were put in each of sixteen ordinary test tubes which were then treated as follows:—

Tubes 1 and 2, added to bouillon one drop of fresh Crotalus venom; mouth of tubes plugged with cotton.

Tubes 3 and 4, prepared same as last, but tube left open (no cotton plug).

Tubes 5 and 6, added one grain of Crotalus peptone. Tube closed by cotton plug.

Tubes 7 and 8, same as last, but tubes left open.

Tubes 9 and 10, added one grain of Crotalus globulin. Tubes closed.

Tubes 11 and 12, same as last. Tubes open.

Tubes 13 and 14, a pure bouillon, nothing added to it. Tubes closed.

Tubes 15 and 16, same as last. Tubes open.

Twenty-four hours later the bouillon in all the test tubes which originally was perfectly clear had become cloudy except tubes 13 and 14 (which contained the sterilized pure bouillon plugged well with cotton).

On the third day of the experiment tubes 3 and 4 (fresh venom, tubes open) showed well-pronounced putrefaction of the bouillon.

Slight putrefactive changes were subsequently observed in the remaining tubes (except 13 and 14) in the following order:—

On the fourth day, tubes 7 and 8. On the fifth day, tubes 11 and 12, also in tubes 15 and 16.

On the seventh day all the plugged specimens were examined, and all showed

more or less putrescence except the tubes with the pure bouillon as stated. Of these closed test tubes, however, tubes 1 and 2 (the fresh venom) showed the putrefactive changes to be much more pronounced than in the remaining tubes; but as we have seen putrefaction ensued much sooner in the tubes that were open (tubes 3 and 4).

As all the tubes showed putrefaction more or less, it is presumable that the *peptone* and *globulin* accidentally contained bacteria, these substances not having been sterilized at the commencement of the experiment.

The contents of the tubes examined microscopically during and at the end of the experiment showed the presence of bacteria of putrefaction in direct proportion to the putrefaction changes.

Imperfect as this experiment may be, it appears to establish the fact that fresh venom promotes putrefactive changes comparatively more rapidly than the venom peptone and globulin, but it also shows further that this power to produce putrescence is very much aided by the action of the air, and depends upon the presence of bacteria contained in that air or in the venom. It was also evident that putrefaction was considerably retarded in all the tubes that were plugged by the cotton, and further that unplugged tubes containing sterilized soup, and exposed to contamination from air showed also putrefaction but at a later date.

Putrefaction Experiment with Muscular Tissue and Venom.—The following rough experiment also appears to show that putrefactive changes develop in dead animal tissues much more rapidly in the presence of venom than without it.

Experiment.—A few drops of a solution of dry Crotalus venom were poured upon a small piece of fresh muscle just removed from the thigh of a rabbit and placed in a covered glass beaker.

A similar preparation but without the addition of venom was made in a second covered beaker. Temp.  $70^{\circ}$  to  $80^{\circ}$  F.

Putrefactive changes began to appear in the specimen treated by the venom after twenty-four hours, and after seventy-two hours were quite far advanced. Under the microscope the muscular tissue showed necrotic alterations very similar to those (to be described later) as occurring in experiments upon the living muscle. A multitude of dumb-bell-shaped rod bacteria, some large bacilli and the micrococci of the venom enormously multiplied, were seen in the decaying muscular substance.

In the specimen of muscle not treated by venom, putrefactive changes were delayed to the fifth day and then appeared to be much less conspicuous, showing but few bacteria. The muscle fibres were uniformly cloudy and degenerated but not broken down in the peculiar manner caused by venom.

Experiments with Bouillon and Venom in Sealed Glass Bulbs, Venom being thoroughly Sterilized.—More satisfactory and conclusive results were obtained from the following experiments:—

A number of small glass bulbs were filled with sterilized bouillon after the well-known method of Dr. Sternberg, and after being thoroughly resterilized by boiling the following preparations were made:—

To each of six bulbs was added one grain of dry Crotalus venom, the venom having been previously subjected to sterilization in a dry heat at 110° C. for one

hour. The bulbs were then hermetically sealed by melted glass. The bouillon in these tubes (with sterilized venom) remained perfectly clear and free from bacteria. Microscopical examination was made at various periods, the last time after eighteen months when it was still perfectly clear and showed no signs of putrefaction.

A similar result was obtained in an experiment with another set of six glass bulbs filled with bouillon, and to which some Moccasin peptone, previously sterilized, was added. These bulbs looked somewhat cloudy, but on examination of the contents eighteen months later no bacteria, and no putrefactive changes were noted.

As a control experiment six bulbs filled with pure sterilized bouillon were kept for a similarly long period, and they all remained clear and free from change; while a few bulbs filled with unsterilized bouillon showed great cloudiness, bacteria, and putrefactive change.

4th. Culture Experiments.—The study of the morphology of the bacteria inhabiting the venom was next undertaken. To this end numerous culture experiments to isolate the bacteria from the venom were made. As stated before, the perfectly fresh venom contained only one form of these vegetable organisms, the micrococci, and only to these latter attention was paid; the rod bacteria and bacilli not

appearing except in venom which had began to putrefy.

The micrococci contained in the venom showed the following behavior in pure cultures: Of culture soils, the peptonized gelatine prepared after the formula of Koch proved to be quite suitable. The isolation of the micrococci was made after the methods of Sternberg and of Koch, as adopted in the pathological laboratory of the University of Pennsylvania. For gelatine culture a minute quantity of venom was smeared on the surface of the solidified jelly contained in a sterilized, small, flat, well covered glass vessel. The micrococci liquefied the jelly, an effect not peculiar to all bacteria. After twenty-four hours all over the inoculated surface of the jelly were seen small turbid drops which contained the micrococci. With a sterilized platinum wire the micrococci from one of the liquefying specks upon the first culture were transplanted to the jelly in a second culture vessel. From this second generation a minute quantity was transplanted to a third and fourth culture vessel. The fourth and all the later generations yielded usually a pure crop of micrococci.

In impure cultures dumb-bell-shaped bacteria and sometimes large bacilli were met with. These, however, could not be said to be peculiar to venom, as they are never found in fresh venom. It may, therefore, be concluded that these cultures represent the micrococci peculiar to, or at least those constantly inhabiting venom. Moreover, the micrococci in these cultures whenever they were successful, were the only bacterium seen and were fully identical as to shape, measurement, and behavior to aniline dyes with those found in the fresh venom.

Much better crops of the venom-micrococci were obtained in bouillon cultures in Sternberg's glass-bulbs. The micrococci grow more rapidly and better in these bulbs, because the bouillon can be heated up to the more suitable temperature of 40° C.; while the jelly cultures could not be warmed to such a degree without melting solid gelatine. A variety of other culture soils and methods of isolation were

employed in these experiments, but their description here is unnecessary as not being sufficiently related to the points at issue.

In relation to the morphology of the micrococci it may be added, that they measure on the average  $\frac{1}{40000}$  of an inch in diameter; they often appear in pairs, but most commonly in zooglæa masses. They show a distinct aureole, such as is met with in various forms of micrococci.

These aureoles have lately been erroneously described by Friedlander, as peculiar to certain "specific" micrococci in croupous pneumonia. In conclusion, it might be said that the venom micrococci do not appear to differ from the micrococci found in the saliva of men and other animals.

In order to test whether the venom-micrococci were in any way specific or pathogenetic, and whether they form, or contribute to, the virulence of the venom, inoculations with pure cultures of the micrococci were made upon animals.

As these experiments gave entirely negative results, it is superfluous to enter into details. Suffice it to say that large quantities of the pure micrococci from a sixth generation were injected, in various manners, into rabbits, cats, pigeons, and white rats, but without fatal results; or without producing any other lesion than occasionally local abscesses, or later on, metastatic abscesses. Sometimes the so-called "miliary tuberculosis of animals" was produced by inoculating with the venom-micrococci. No signs of any lesions resembling those of venom poisoning were observed.

Experiments made to Study the Anatomical Changes produced by the Venom in living Animals. Naked Eye Appearances.—Very many years ago Dr. Weir Mitchell described two forms of venom poisoning—rapid or acute, and slow or chronic. To the latter appear to be relegated by him all those cases in which death is protracted beyond a few hours. This convenient division is justified by certain differences in the mode of termination of venom poisoning, and by the macroscopic and microscopic appearances of the lesions induced.

In the most rapid poisoning, there is frequently nothing appreciable to the naked eye beyond the slight local lesion or here and there minute capillary hemorrhages, when death has been delayed beyond a minute. In examples of chronic poisoning both the local and the systemic changes are enormously more extensive. When animals were subjected to chronic poisoning they were kept under the influence of narcotics, since it had been learned that these agents did not affect the results. No Cobra venom was employed in this series, but only the pure or dried venoms of our own serpents, or else some one or other of the constituents of these poisons.

The following tables relate the experiments made, and the more striking morphological changes:—

<sup>&</sup>lt;sup>1</sup> See "Memoir on Diphtheria," Report to the National Board of Health, 1882, by H. C. Wood and H. F. Formad.

#### RAPID POISONING.

Effects of Venom when Injected Hypodermatically into or Applied otherwise to the Tissues of the Living Animal.

No. of expt.	Animal used.	Form and quantity of venom, and where introduced.	Time of death.	Local lesion.	Condi- tion of blood,	Changes in thorax, abdomen, brain, and membranes.	Remarks.
1	Pigeon	Crotalus venom, fresh, ¼ grain in- jected into pecto- ral muscle	Killed after 5 minutes	Moderately sized, dark hemorrha- gic swelling	Coagu- lable and red	All internal organs congested; no other changes visible; no ecchymoses perceptible	This animal was killed before the full effects of the venom.
2	Pigeon	Same as last	Died in 15 minutes	Very dark colored hemorrhagic swelling	Less co- agulable and quite dark	Organs only moderately con- gested, but there were nu- merous small subpleural, subperitoneal, and slight subpericardial ecchymoses	For the details and the his- tological appearances, see the next chapter. The studies of the changes in muscular tissue were mostly made from this experiment.
3	Pigeon	Moccasin venom, fresh, 1 drop in- jected into peri- toneum	Died after 1 hour and 50 minutes	Profuse hemor- rhage all over peritoneal cavity	Liquid very dark	Ecchymoses in nearly all organs, quite marked in arachnoid and at base of brain; some so small as to be visible only by microscope. Extreme congestion	•
4	Pigeon	Crotalus venom, fresh, 1 drop into peritoneum	Died in 25 minutes	Same as last	Liquid dark	Hemorrhages only subperito- neal, other organs merely congested	
5	Rabbit	Moccasin venom, injected into peri- toneum	9 minutes	Subperitoneal hemorrhages	Coagu- lable on exposure	No changes beyond local lesion	
6	Pigeon	Peptone, injected into pectoral muscle	35 minutes	Hemorrhagic swelling	Liquid	No visible changes, except all organs congested	Changes in muscular tis- sue similar to those pro- duced by fresh venom, but far less blood effused.
7	Pigeon	Moccasin venom, fresh, injected into cavity of skull	5 minutes	Hemorrhages in arachnoid and brain tissue	Slightly coagu- lable	Membranes of brain and brain substance peripherally soak- ed with blood; other organs congested	
8	Rabbit	Moccasin venom, fresh, ½ grain in- jected into lung	1 minute	Lung infarcted by blood	Same as last		See specimen and descrip- tion in chapter on histo- logical changes.
9	Rabbit	Peptone, ½ grain into liver and peritoneum	43 minutes	Ecchymosis locally only	Liquid dark	Other organs not visibly affected	
10	Rabbit	Same as last	Killed at the end of 1 hour	Slight subperito- neal ecchymoses	Dark, but co- agulable	No systemic changes.	
11	Pigeon	Peptone, 1 grain into peritoneum	20 minutes	Local ecchymoses slight	Ditto	No notable changes in other	Histological changes similar to those pro-
12	Pigeon	Globulin, ½ grain into peritoneum	40 minutes	The same as last	Ditto	organs	duced by fresh
13	Cat	Crotalus globulin,  grain into peri- toneum	40 minutes	Profuse ecchy- mosis	Slightly coagu- lable	Hemorrhage only local	Venous.
14	Cat	Crotalus peptone,  \frac{1}{2} \text{ grain into peritoneum}	1 hour and 20 minutes	Same as last, but less marked	Liquid	Hemorrhage only local, also extreme congestion of all organs	Microscopic examination made of every organ. The details will be
15	Rabbit	Crotalus globulin,  ½ grain into peri- toneum	Killed in 10 minutes	Same as last	Red and coagu- lable		given hereafter.
16	Rabbit	Dry Crotalus  venom, ½ grain in  watery solution, into peritoneum	Killed in 10 minutes	Same as last	Same as last	Same as last	
17	Rabbit	Dry Crotalus venom, & grain in watery solution, into peritoneum	Died 1 hour and 25 minutes	Same as last	Very dark, liquid	Ecchymoses in all organs ex- amined. Profuse ecchymo- ses in peritoneum, also sub- pleural, subarachnoid, and subpericardial. Liver, which was injured by the syringe, showed a large hemorrhagic infarction	

#### RAPID POISONING -CONTINUED.

No. of expt.	Animal used.	Form and quantity of venom, and where introduced.	Time of death.	Local lesion.	Condi- tion of blood.	Changes in thorax, abdomen, brain, and membranes.	Remarks.
18	Cat	Dry Crotalus venom, 1 grain in watery solution, into peritoneal cavity	Died 5½ hours	Same as last	Same as last	Peritoneal cavity contains a good deal of liquid blood; hemorrhage at base of brain (subarachnoid); no other lesion noted; organs rather anæmic. Heart empty, con- tracted	Cats appear to resist the effects of venom much longer than the other animals used in this research.
19	Cat (chlor- alized)	Peritoneum opened, mesentery exposed uninjured, in moist chamber, and smeared repeatedly with a solution of dry venom, using not less than 5 grains of venom	Died after 4 hours and 35 minutes	Hemorrhagic in- filtration, quite extensive, but came on very slowly	Partly coagu- lable	Peritoneal hemorrhage; or- gans anæmic	It appears that when the mesentery is exposed and not injured the animal survives much larger applications of venom than if venom be injected into an unopened peritoneal cavity. Very small quantities of venom appear to kill in the latter case. For further experiments of this character, see Mechanism of Hemorrhages.

None of the cases in the table exhibit instances of the greatest possible rapidity of death. Dr. Mitchell has seen a pigeon die within ten seconds from a hypodermatic injection of pure Crotalus venom. In such a case there is positively no lesion, and the blood is solidly coagulated.

In most cases very soon after injection of the venom in either of its forms, the time varying from a few minutes to a few hours, according to the kind of animal and the quantity of venom used, there appears a swelling at the point of injection with intense violet-black discoloration of the skin, which gradually extends over an area of several square inches. On making an incision into the tissues in the immediate neighborhood of the injection, they are found to be soaked with extravasated blood. This is often all that is visible if death has occurred soon; but if it has been postponed for a short time, then in tissues distant from the place of the injection, extravasations to a smaller extent were often found. Most pronounced and most frequent are the ecchymoses below serous membranes (subpleural, subperitoneal, and subpericardial); in fact the whole organism is deeply affected, the tissues being congested and presenting a much darker appearance than normal. The blood does not seem to coagulate readily within cavities or interstices of the body unless death follows almost instantaneously. In cases which live longer, the blood remains commonly in a liquid state, or coagulates imperfectly, and then only after being exposed to the air, resembling in this particular the state of that fluid observed in conditions of asphyxia.

# SLOW POISONING. Effects of Venom upon the Tissues of the Living Animal.

No. of expt.	Animal used.	Form and quantity of venom, and where introduced.	Time of death.	Local lesion.	Condi- tion of blood.	Changes in internal organs.	Remarks.
20	Pigeon	Copper globulin, 2 c. c. (equal to 1 gram fresh venom) injected into pec- toral muscle	13 hours	Large, dark gan- grene like swell- ing of chest; muscle disinte- grated	Liquid and dark	Subpericardial ecchymoses and pericardial effusion. Red tinged serum in peritoneal cavity. Heart empty. Lungs and pleura full of ecchymoses. All the organs congested	
21	Rabbit	Unknown, but very minule quantity of Crotalus venom injected in back	9 days	Dark gangren- ous swelling	Liquid and dark	Numerous minute hemorrhages be- low serous membranes, seen also at base of brain in right posterior fossa. The organs rather anæmic and softened	All these autopsies were made immediately or quite shortly after death.
22	White rat	Crotalus venom, dry, ½ grain in- jected into abdo- men	2 days and 7 hours	Hemorrhagic peritonitis	Slightly coagu- lable, dark	Organs congested, softened; nothing else peculiar found; small, loose, red clot in right side of heart	For changes in blood, see details in text.
23	Cat	Crotalus venom, dry, 1 grain in- jected into right thigh	9 days and 2 hours	Skin slough over local lesion, which is dark, hemorrhagic, and gangrenous	Liquid dark, ill smelling	All internal organs softened and highly eachymosed and congested. Feces and urine bloody. Hemor- rhage at base of brain, and min- ute blood specks in pericardium. Heart quite atrophied and softened	
24	Pigeon	Quantity unknown, injected into pec- toral muscle	14 days	Atrophy, with pigmentation of the pectoral muscle injected	Liquid and very dark	Hemorrhages indicated by deposits of blood pigment in the tissues. All the organs in a state of atrophy and softened, resembling acute yellow atrophy in man. Serous sacks all distended with bloody serum. Heart empty, and although contracted quite soft	For further details of the histological changes, see text.  N. B.—Gangrenous changes in the local lesion are usually more pronounced in the "Slow" than in the Rapid form of venom poisoning.

The following lesions may be mentioned as peculiar to retarded or slow poisoning: Rigor mortis often absent. The blood, usually diffluent, is very dark and does not readily acquire the scarlet-red color when exposed to the air. There are prominent blood-stained effusions in all the serous sacks. (Plate V.) Urine and fæces often bloody. Hemorrhages beyond the local lesion much more conspicuous than in the rapid poisoning. The remote lesions of slow poisoning resemble very much (morphologically) the primary local lesion, but are not so extensive or so well defined. In general the conditions of slow venom poisoning resemble those of acute septic poisoning. It is very often impossible to draw a distinct line between the manifestations of rapid and slow poisoning, nevertheless the division is in practice convenient.

One case of very protracted slow poisoning was observed in a pigeon which had been injected with venom in the pectoral muscle. (See Experiment 24, Table Slow Poisoning.)

Instead of the usual gangrenous change there was seen in this case after the lapse of two weeks a decided dry atrophy of the muscular tissue about the wound. Its fibres were greatly diminished in size as compared with the opposite unaffected

muscle, and many of them were entirely disintegrated, as was evident from the remnants of the muscular fibres and the granular material which took their place between the interstices of the connective tissue. This granular material was seen throughout the specimen, some of it being of a brown tint, and probably representing disintegrated blood corpuscles. The internal organs were all in a state of atrophy, more particularly so the liver, the tissues of which under the microscope bore a striking resemblance to acute yellow atrophy. The serous sacks were all largely distended by blood stained serum. The heart muscle was also in a condition of atrophy, its chambers empty, and the blood dark and not coagulable. Blood examined microscopically showed appearances to be mentioned shortly.

The Effects of certain Venoms on the Coagulability of the Blood.—One of the most interesting differences in the action of the venoms of the Rattlesnake and Cobra and which was pointed out some years ago by more than one observer, is that the former venom partially or completely destroys the coagulability of the blood, while the venom of the Cobra has no such marked effect. The blood of animals poisoned with Crotalus venom is usually thin and dark, the clots form slowly, and are very soft and easily broken up.

Some direct studies were made to test more accurately this interesting property of the Crotalus venom, and it was thus observed that it is not peculiar to the poison of this genus, but is also a characteristic of the Moccasin. Several of these observations which were made with the venom of the *Crotalus adamanteus* we record in detail.

Experiment.—Five test-tubes were used:—

No. 1 empty.

No. 2 contained  $\frac{1}{4}$  grain dried venom dissolved in 0.5 c. c. distilled water.

No. 3 " 
$$\frac{1}{4}$$
 " " in 1.0 " " No. 4 "  $\frac{1}{2}$  " " in 1.0 " "

No. 5 " 2 drops glycerine solution of venom, equal parts.

These test-tubes were packed in snow, to retard coagulation and to give the venom a better opportunity to act, the tubes remaining in this condition for about half an hour. The main artery in the leg of a large etherized rooster was exposed, and a canula placed in it. The blood was allowed to flow into the tubes in the order of their numbers, the tubes being gently shaken to mix the venom and blood. The operation began at 3:55 and ended at 4:00 p. m. At 4:35 the tubes were examined. The blood in No. 1, which contained no venom, was firmly clotted, in all the others the blood was fluid. At 4:55 the test-tubes were all taken from the snow. Blood in No. 1 was firmly clotted and of a bright-red color; blood in Nos. 2, 3, and 4 was fluid and venous in appearance; blood in No. 5 was fluid and of a brighter red than No. 1. The tubes were then corked with raw cotton and set aside.

Twenty-four hours later blood in No. 1 was firmly clotted, in Nos. 2 and 3 tarry, in No. 4 tarry, but thinner than in Nos. 2 and 3, in No. 5 perfectly fluid; in the lower half of the tube was a mass of corpuscles, while the upper half had the appearance of pure serum.

Forty-eight hours—no appreciable alteration.

Seventy-two hours—no appreciable alteration; the blood in tube No. 1 had no unpleasant odor, but all the rest gave decided odors of putrefaction, and were very dark.

Comparative observations were also made at the same time with different venoms, using as before a fowl to furnish us the blood and the snow pack to retard coagulation

In test-tube No. 1 was placed  $\frac{1}{2}$  grain dried Moccasin venom in 1 c. c. distilled water.

In test-tube No. 2 was placed  $\frac{1}{2}$  grain dried Moccasin venom *boiled* and filtered through clay.

In test-tube No. 3 was placed  $\frac{1}{2}$  grain of dried Crotalus venom in 1 c. c. distilled water.

In test-tube No. 4 was placed  $\frac{1}{2}$  grain of dried Crotalus venom in 1 c. c. distilled water, heated gradually to 70° C.

In test-tube No. 5 was placed  $\frac{1}{2}$  grain dried Cobra venom in 1 c. c. distilled water. In test-tube No. 6 was placed  $\frac{1}{2}$  grain dried Cobra venom in 1 c. c. distilled water, boiled and filtered through a clay filter.

In test-tube No. 7 nothing was placed but the pure blood.

Into each of the test-tubes about 10 c. c. of blood was allowed to flow; at the end of 15 minutes the blood in Nos. 2, 5, 6, and 7 was clotted firmly, and the blood in Nos. 1, 3, and 4 was perfectly fluid. After one hour and a quarter the blood in No. 1 was clotted in a quite remarkable clot, which was exceedingly elastic—the clot when picked up and suspended drew out into a long worm-like thread, and could then be further pulled out to at least double its length, resuming its natural size when placed upon the table. The blood in No. 3 had some very soft clots. In No. 4, the blood was clotted soft.

On the second day all of the bloods were firmly clotted except Nos. 1, 3, and 4, which were perfectly fluid and had a putrefactive odor, which was absent in the others. On the third day these bloods were clotted and had some dark serum, but the pure blood was clotted firmly and perfectly dry on the surface.

From these observations it seems clear that the Cobra venom exerts no appreciable effect on the coagulability of the blood of a chicken when thus circumstanced, and that Crotalus and Moccasin venoms act powerfully. Moreover, that the effect of the Crotalus venom is the more efficient, and that if the solutions of venom have been subjected to a degree of heat sufficient to coagulate the venom-globulins, the effect is lessened very greatly. It thus appears that the principle affecting the coagulability of the blood is most largely the globulin.

It would seem therefore that venom-peptone, although not without power to lessen the coagulability of blood, has not the full efficiency of the globulins. Neither can it be said as to this capacity, that the small percentage of Cobra globulin has even relatively the anti-clotting capacity of the globulins of Crotalus.

These differences between Cobra and Crotalus show themselves strikingly in the slighter local disorders caused by the Indian serpent.

The singular formation of an elastic clot was observed in other cases. It appeared to be a temporary condition, and to be in a measure due to the great increase in the adhesiveness of the blood corpuscles.

Microscopical Changes in the Various Tissues of the Body from the Effects of the Venom of Crotalus.

Effects of Fresh Venom upon the Blood Corpuscles.—A series of experiments were made to study the direct as well as the remote effects of the venom upon the blood corpuscles. The result of these observations was the discovery of some changes which have not been heretofore fully described.

A drop of blood from man or any mammal treated with a minute quantity of fresh venom, presented the following appearances under the microscope: Upon the white blood corpuscles, the venom did not appear to have any other effect than to stop the amœboid motion, which in presence of venom could not be kept up, even by the use of the warm stage. The cells appeared somewhat larger than usual and also more granular. The red blood corpuscles appeared unchanged when observed, but for a moment, and superficially, yet prolonged and careful study revealed very remarkable alterations. The alterations in the red blood corpuscles are essentially these:—

The blood disks lose their biconcavity and assume a spherical form, but without parting with their coloring matter. They exhibit also great adhesiveness, arranging themselves into various sized and shaped aggregations. The corpuscles comprising these groups sometimes appear to fuse so that their outlines cannot be determined, even by high amplification. In addition the corpuscles seem to soften and acquire a peculiar ductility and capacity to be stretched without fracture. By inclining the stage of the microscope, or making gentle pressure upon the coverglass, allowing thereby the liquid to flow, the red blood corpuscles may be seen to clongate themselves into spindle-shaped or even into fine thread-like bodies. (Figs. 1 and 2, Plate III., and Plate IV.) Such masses of corpuscles appear to act like colloid material.

One drop of human blood was mingled with one of fresh snake venom by the application of the cover-glass. The three fields photographed were found in the zones of contact between the blood and venom; they occurred within a small area—almost adjacent. Fields 1, 2, and 3, Plate IV., were photographed respectively within 15, 30, and 40 minutes after the first application of the venom to the blood. As the masses of corpuscles were slowly changing form and position, the exposure was, necessarily, but for a part of a second. The lens employed was Spencer  $\frac{1}{10}$  immersion, giving 400 diam, with the low power eye-piece.

This remarkable condition seems, however, to be only temporary, and in fact often escapes observation. After a short time, which in about 100 observations was found to vary from a few seconds to a quarter of an hour, the apparently homogeneous blood-cell masses break up anew into individual corpuscles, which then continue isolated or in bead-like rows, but remain spheroidal, *i. e.*, do not regain their biconeal shape.

Those corpuscles which arrange themselves in rows present an appearance strikingly different from the ordinary rouleaux arrangement of normal blood-disks, an appearance which may better be designated as "beaded," because the corpuscles are here spheroidal and not disk-like.

Liquids in general variously modify the shape of the red blood-disks, but no liquid or reagent tried in control experiments produces the effects described above.

Watery solutions of dried venom did not exhibit the immediate influence upon the red blood corpuscles as well as the fresh venom, although the corpuscles very promptly became spheroidal as they do from most watery liquids; but did not lose the coloring matter as when exposed to pure water without venom.

The blood of birds, upon being mixed with venom, does not show the above described changes in as striking a manner as mammalian blood. The nuclei of the oval corpuscles of the pigeon appear, however, to undergo a rapid necrotic change which finally gives rise to a granular albuminoid material to be seen floating in large quantities between the corpuscles.

A number of experiments were made to study the changes in the corpuscles of the living animal. Fresh venom or solutions of dry Crotalus venom were injected hypodermatically, and then the blood taken at intervals from the local lesion as well as from the general circulating fluid and examined under the microscope.

The blood taken from local lesions presented quite often alterations in the corpuscles similar to those observed in a direct mixture of blood and venom under the microscope, as described above. It was not possible, however, to trace all the modifications of the red blood corpuscles in specimens of the circulating blood; only one change being constant, viz., the spheroidal transformation of the blood disks. The red blood corpuscle retained the acquired spherical shape after the death of the animal.

All the experiments made in order to study the ultimate changes in the blood-corpuscles gave nearly similar results varying slightly in degree with the quantity of the venom and the animal employed. The record of one observation will suffice for all

Experiment.—Young cat. Injected at 2 P. M. 3 m. m. fresh Crotalus venom in

left thigh. Hair of part being previously clipped away.

2 minutes later. Animal well. Blood microscopically examined. Local lesion; blood-disks assuming spherical-shape. Blood from auricular artery showed no changes in the blood-disks.

5 minutes later. Animal well. Local lesion; blood-disks all spherical showing also gelatinoid behavior and ductility on pressure. Auricular artery, blood-disks pormal

8 minutes later. Animal restless. Local lesion shows only spherical shape of red blood-disks. Auricular artery also shows partial change of red blood-disks to spherical shape.

12 minutes later. Animal ill. Blood of local lesion as well as blood taken from jugular vein shows same changes as when last examined.

<sup>&</sup>lt;sup>1</sup> Errors in distinguishing the spheroidal shape of the red blood-corpuscles from the round shape which the normal disk-like corpuscles exhibit when viewed in a certain position are easily eliminated when the blood is brought into current by gentle pressure upon the cover-glass, or by inclining the stage of the microscope. The disks assuming spheroidal shape are decidedly reduced in diameter and appear smaller.

20 minutes later. Animal quite ill. Red blood-disks all spheroidal when examined in the local lesion and in several other parts of the body.

25 minutes later. Animal dead.

30 minutes later. Blood examined from heart. All the red blood-disks spherical.

24 hours later. The dead animal being kept in a cool place. Red blood-disks all spherical and many disintegrated.

The blood, in sections of tissues from animals poisoned with venom, also presents decided alterations. The corpuscles in tissues hardened with preserving fluid are seldom seen intact. When, however, the parts in question are placed in preservative fluid immediately after the death of the animal the spheroidal (altered) red blood corpuscles may be distinguished; and still more likely are they to be intact if the animal was killed before the venom had asserted its fatal effect.

The corpuscles as a rule appear disintegrated in animals dead from slow Crotalus venom poisoning, and present themselves as a granular débris of a yellowish or dark brown color. The tissue elements of the part into which the venom had been directly injected are as a rule profusely saturated with the coloring matter of the blood. The microscope further reveals blood crystals and numerous bacteria between and within the tissue elements. This indicates the profound alteration which takes place in the blood in venom poisoning, and accounts for the black appearance and the rapid putrefactive changes which are seen in the local lesion.

"Quite recently Lacerda, in lectures' on snake poisons, speaks of alterations of the blood, which differ much from those observed by us. He does not state the serpent venom employed. It was presumably from the Bothrops wrutu, Lacer. In slow poisoning, he says, the blood globules become indented like a toothed wheel. Some are elongated, deformed, or broken up; others present shining points and then break up into minute fragments. Some undergo a change of tint to chesnut brown, others become entirely discolored.

"The consequences of mixing pure blood and pure venom, he says, are these: The red blood-globules unite in mass, adhere one to the other and begin thereon to lose their normal forms. In a few minutes the dissolution is complete. There remains only an amorphous protoplasmic matter, semi-liquid, diffluent, of a uniform yellow color, with well-marked red striations. After some minutes the hematine or coloring matter quite disintegrated is seen under the form of granular substance of a deep vermillion red. Whilst the globules thus break up bubbles of gas rise here and there,"

We have quoted this account nearly in full to point out that it describes a sequence of appearances very unlike those which we have delineated.

Effects of the Venom upon certain Tissues.—Direct observations were further made as to the effects of venoms upon the various solid tissues, such as the bloodvessel walls; muscular tissue, unstriated and striated; nervous tissue (brain and medulla

¹ Leçons sure le Venin des Serpentes du Brésil, etc. J. B. De Lacerda, pp. 87-88. Rio de Janeiro, 1884.

<sup>19</sup> June, 1886.

oblongata); lungs, liver, skin, mucous membranes, the cornea, spermatozoa and ciliated epithelium, and most extensively upon the mesentery and other serous membranes.

If fresh venom be injected into any organ or applied to any internal part of the body, one of the chief effects is, as Dr. Weir Mitchell showed twenty-two years ago, the production of minute hemorrhages.

The studies reported here thoroughly confirm Dr. Mitchell's observations. Above all, it was further evident that, as a general rule, it was everywhere the parenchymatous elements of the organ or parts that underwent necrotic changes (which will be described below), while the interstitial elements of organs or tissues acted upon by the venom, remained usually unaffected, or were merely infiltrated with blood, or with the disintegrated products of blood.

Effects of Venom upon Bloodvessel Walls.—If fresh venom be applied to a vascular tissue and watched under the microscope, no effect upon any of the larger bloodvessels is perceptible. It appears that the venom even after prolonged contact has no visible influence upon the smooth muscular tissue constituting the middle coat of arteries and veins. The adventitia of such vessels also offer considerable resistance, although the vasa vasorum become extremely congested. Even small arterioles and venules are unaffected.

The capillary bloodvessels, however, having a mere endothelial wall surrounded by a delicate adventitia show a decided change upon the application of venom. The endothelium constituting the capillary wall becomes cloudy and looks as if roughened and displaced, and though no actual rupture of the vessel is demonstrable to the eye a diapedesis of blood-corpuscles and a leakage of serum occurs, and this process is sometimes amazingly rapid. As will be described later with more details, the following are the essential points in the action of the venom upon its direct application to a vascular membrane viewed under the microscope. The blood current appears at first to be accelerated, and the color of the blood becomes darker. Then in a few moments while the circulation still continues in the veins and arteries, in many of the capillaries stagnation occurs. From these latter vessels, and apparently only from them, the blood oozes, first forming pin-point ecchymoses which gradually increase, and which by fusion give rise at last to a general hemorrhagic infiltration of the neighboring tissues.

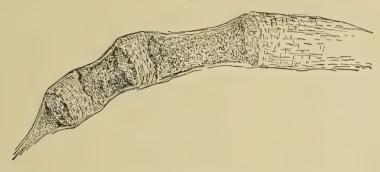
Changes in the Striped Muscular Tissues.—Venom directly applied to living striped muscular tissue produces changes which become apparent immediately after the death of the animal. The ultimate muscular fibrillæ readily break up into their sarcous elements, these becoming easily separable in transverse layers, the so-called Bowman's disks. A granular change of the elements, not however uniform in character and distribution, is quite conspicuous. (Fig. 3.) It should be noted that all these changes occur without the addition of any other reagent than venom and become conspicuous when the poisoned tissue is teased out in water.

The alterations just referred to are most manifest in muscular fibres near or around which the capillaries are affected by the venom, localities apt to be marked

<sup>&</sup>lt;sup>1</sup> Figured by Dr. Mitchell, in his first essay.

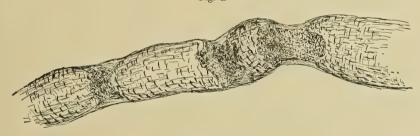
by the presence of extravasated blood. The changes described are not uniform, even in an individually affected fibre, but are bounded by small abrupt layers of

Fig. 3.



normal sarcous elements, the whole being surrounded by an unaffected sarcolemma. The latter, which is beautifully demonstrated on such occasions, shows constrictions in those places where the sarcous elements are disintegrated. (See Figs. 3 and 4.)

Fig. 4.



All muscular fibres of the part where the poison was injected are more or less granular, and are often stained by hematin. The granular material between the fibres has very much the appearance of micrococci, but by appropriate tests only a small proportion of the granules can be identified as bacteria. The remaining granular matter can be identified as particles of necrosed sarcous elements, disintegrated blood, and granular substances which have been described as constituents of the fresh venom and introduced from without. These granular muscle changes occur only in or near the wound, and not also in remote muscles. They demand for their production a certain length of time, and are most decided in cases of long survival.

Changes in the Lungs.—As has been seen from the table of experiments, the injection of venom into the lungs was followed by nearly instantaneous death. The local lesion was an hemorrhagic infarction throughout the whole of the paren-

chyma, filling also all of the air vesicles. There were extensive sub-pleural ecchymoses, both parietal and visceral, as well as sub-pericardial ecchymoses. Under the microscope with high amplication sections of the lung tissue showed a peculiar clogging, fusion, and ductility of the red blood-corpuscles not unlike that which follows the application of fresh venom to the blood.

This appearance is, however, not uniform, as in many places the corpuscles are merely spheroidal, or have undergone a granular disintegration. The bloodvessels are all highly congested, the air vesicles seem to be distended by extravasated blood. The micrococci introduced with the venom appear to have rapidly multiplied, numerous masses being seen in the air vesicles and in the more necrosed parts of the lung tissue. In general the tissue is deeply stained by the coloring matter of the blood.

Brain and Medulla Oblongata.—If a minute quantity of venom was successfully injected directly into the cranial cavity of a pigeon, the animal fell immediately and expired in a few minutes. The pia mater was preëminently the seat of hemory rhages, and blood was also seen to fill the peri-vascular spaces of many of the cerebral vessels. The cerebral tissue, and particularly the nerve elements, showed a granular change analogous to that observed in muscular tissue, and similar appearances were noted from the effects of the venom upon the medulla oblongata and spinal cord. Where animals were poisoned by introducing the venom subcutaneously into some other part of the body, minute capillary hemorrhages were also observed in the membranes of the brain, and in two instances ecchymoses were noted in the substance of the medulla oblongata, although as a rule only intense congestion of its vessels was seen. The bloodvessels were so much distended with blood as to be double or even triple their normal calibre, fully obliterating the perivascular spaces and unquestionably exerting much pressure upon the surrounding nerve elements.

Effects of the Venom when applied to Uninjured Mucous Membranes, and upon the Cornea.

The following experiments were made:—

Experiment.—Adult albino rabbit, etherized. A drop of an aqueous solution of the dried venom Crotalus adamanteus was dropped on the cornea and conjunctiva of the left eye. In a few minutes the conjunctiva became ecchymosed and ædematous to such an extent as to close the eyelids. Animal died in five hours. After death the conjunctiva and eyelids were seen to be soaked with extravasated blood, while the cornea remained perfectly transparent and colorless, showing no trace of inflammatory change when removed and examined under the microscope.

Post-mortem examination showed extensive sub-pleural, sub-peritoneal, and slight sub-arachnoid ecchymoses.

Experiment.—Young kitten, etherized. A drop of fresh venom was placed on the cornea. Results, similar to those of foregoing experiments, the cornea remaining transparent, but exhibiting a certain roughness upon the surface, which under the microscope proved to be due to slight desquamation of the epithelium.

Experiment.—Young kitten, etherized. Abdominal cavity and stomach opened and fresh venom applied to surface of mucous membrane. Specimen watched for half an hour failed to reveal any decided visible changes, beyond a slight corrugation and congestion. No ecchymoses.

The Effect of Crotalus Venom upon Ciliary Motion.—Fresh venom applied to ciliated epithelium taken from the edge of the tunic of a fresh oyster seemed to exert no effect upon ciliary motion. The specimen was watched and compared with the control experiment side by side. The ciliæ still kept up their movement at the end of three hours in both specimens.

Fresh venom was applied to ciliated epithelium taken from the pharynx of a live frog. The specimen was carefully observed and compared with similar preparations in which venom was not used. In the latter the ciliary motion, as a rule, kept up longer. Yet after one hour specimens treated with venom continued to exhibit motion though less vigorous than in the control specimens.

The Effect of Venom upon Spermatozoa.—Fresh venom applied to spermatozoa taken from a live rabbit seemed to exert a decided influence. Specimens treated with the venom were examined side by side with control specimens, and while in the presence of venom the spermatozoa ceased to exhibit their peculiar movements in from one-quarter to three-quarters of an hour, unpoisoned spermatic particles continued to move for many hours. The venom did not appear to produce any changes in the substance or the bodies of the individual spermatozoa.

The Mechanism of the Hemorrhages as Observed in Venom Poisoning.

In order to study the mechanism of the hemorrhages Dr. Mitchell's original observations were repeated as follows:—

The animals used were cats, rabbits, pigeons, white rats, and frogs. The frogs do not give satisfactory results as they withstand the effects very strenuously and if peritoneal hemorrhages occur at all they are very scanty. The most satisfactory observations were obtained when cats were employed, as these animals lived longest after the application of the venom, the latter also acting more slowly, thus permitting satisfactory study of the effects under the microscope.

Anæsthetics were always used. Ether was found to give the best results. Chloral appeared to retard the effects of the venom. While in an etherized animal peritoneal hemorrhages appeared at once upon the application of the venom, in a chloralized animal they occurred much later, and sometimes failed to appear.

A few drops, three to six, of a saturated solution of chloral hydrate were usually sufficient to anæsthetize a small kitten or rabbit, two drops for a white rat, one drop for a mouse. It was administered hypodermatically. In administering ether the animal was placed under a bell-glass, with a sponge kept saturated with the agent until the animal was rendered powerless.

In experiments upon the mesentery to be examined under the microscope, the

<sup>&</sup>lt;sup>1</sup> The observations were made under an amplification of one thousand diameters.

animal was placed on its right side upon a thin oblong wooden board. On one side of the board near the middle was cut a triangular opening, each side being about one inch in length. An incision was then made in the median line through the abdominal integuments, sufficiently large to allow a loop of the intestine to be extracted. Care was taken that pressure should not interfere with the circulation. The loop being drawn out, it was stretched over the hole in the board above described, and kept in position by means of pins.

The venom was applied to the uninjured surface of the mesentery. A saturated aqueous solution of the dried venom was most commonly used. The moist chamber was not required, as the experiments were of short duration. The warm stage seemed only to hasten the process and otherwise was observed to have no special influence, being rather disadvantageous.

Experiment 1.—A young kitten was secured by means of ether as above described, and placed upon the microscopic stage. A few drops of an aqueous solution of the venom were allowed to flow over the mesentery. The part being carefully watched with the naked eye, it was noticed that after one minute tiny hemorrhagic points made their appearance here and there, all over that part of the mesentery which was under the direct influence of the venom. These hemorrhages increased rapidly in size, and in a few minutes the whole surface became the seat of one diffused hemorrhagic infiltration. (Plate III., Figs. 3, 4, 5, 6, 7.)

Experiment 2.—Young white rat. Ether. Aqueous solution of venom applied as before to the mesentery. The loop of the mesentery acted upon was quickly cut out by means of scissors after the lapse of one minute and subjected to drying. A beautiful preparation was thus obtained, in which the minute hemorrhages were permanently fixed by drying, preserving their natural appearance.

Experiment 3.—Young kitten. Chloral. Mesentery spread upon microscopical stage. An aqueous solution of dried venom applied in the same manner as above. In this case the hemorrhages did not appear so promptly and were not so rapid in their development. Nearly five minutes elapsed before they began to form.

Experiment 4.—Young white rat. Chloral. Venom applied as in preceding experiments; there seemed to be delay in the appearances and development of the hemorrhages.

Further enumeration of this class of observation is unnecessary, as more than forty experiments exhibited the characteristic hemorrhages, except in the case of frogs. Five of the latter were used.

It was noted that chloral always retarded the production of hemorrhages, at least they did not appear as rapidly as when ether was used.

Microscopical Details.—It being necessary to study the exact location of the hemorrhages and the mode of the escape of blood, the following modifications of methods were adopted in repetition of the older experiments of Dr. Mitchell.

<sup>&</sup>lt;sup>1</sup> After much experimentation this method of preparing permanent specimens was found to be the only available one. Specimens of mesentery mounted in any kind of liquid very soon lose their proper appearance, as the hemorrhagic specks in the membrane gradually vanish, or get blurred from the effects of the preserving fluid.

Experiment 5.—Cat. Ether. Mesentery exposed and placed on the stage of the microscope. The aqueous solution of venom was applied, and the experiment watched under a magnifying power of 60 diameters. In thirty seconds minute hemorrhagic points were noticed as in all the previous experiments first along the sides of the smallest capillaries. It was also observed that the hemorrhages occurred first in those small capillaries which were in the neighborhood of larger vessels. In vascular plexuses which started from the greater arteries the hemorrhages appeared much sooner than in those which took their departure from smaller arterioles. In each case, however, it was only the capillaries from which the hemorrhages proceeded, the arteries and veins remaining intact. The hemorrhages being seen to proceed from capillaries in the vicinity and along the route of larger vessels, one may erroneously get the impression that it is the latter from which the bleeding arises. No actual breech of continuity in the capillaries was observed, and it appeared as though the blood filtered through the walls of these minute channels.

Experiment 6.—Kitten. Ether. Mesentery exposed in the usual manner. The mesenteric vessels, both the main artery and the veins, were ligated near the root of the mesenteric attachments. A salt solution stained by aniline blue was injected into the vein. The venom was applied, and the field closely watched under the microscope. No extravasation of the injected solution or of blood could be observed.

Experiment 7.—Kitten. Ether. Vessels ligated and salt solution with aniline injected as in previous experiment. Applied aqueous solution of the dry venom. No extravasation of the colored liquid or blood observed.

Experiment 8.—Kitten. Animal secured as before, but no salt solution injected. Mesenteric veins and the artery ligated near root of mesentery. Solution of dried venom applied. Hemorrhage as usual, but slow and scanty.

Experiment 9.—Kitten. Ether. Animal fixed as in last experiment upon microscopical stage. Fresh venom applied and watched for one-half hour. Hemorrhages were seen to develop more slowly.

Experiment 10.—Kitten. Ether. Mesenteric vein and artery ligated as in preceding experiments. Fresh venom applied as before, and a marked delay in development of hemorrhages again observed.

Experiment 11.—Kitten. Ether. Mesenteric vessels tied not only at the root of the mesentery, but also peripherally at the convex portion of the loop, thus almost entirely cutting off the circulation. Fresh venom applied. Hemorrhages were scarcely appreciable with the naked eye.

Experiment 12.—Kitten. Ether. Mesenteric vessels tied at both root and periphery of mesentery. Venom applied immediately. Hemorrhage hardly perceptible.

The above experiments were subsequently repeated, especially those in reference to the effects of the venom upon bloodvessels when blood had been substituted by a 0.75 per cent. saline solution. These experiments, however, gave the same results as those just described, and hence it is unnecessary to occupy space in multiplying similar records. Yet some studies in the same direction have been left undone. It might be desirable to elaborate the methods of experimentation, e. g., by application of artificial blood pressure, etc. In all the experiments above quoted,

except in experiments 6 and 7 (where the blood was substituted by another liquid), the peculiar extravasations of blood followed the application of the venom.

When the mesenteric vessels were tied as in experiments 8, 9, and 10, there was a delay in the appearance of the hemorrhages. When the vessels were tied in two places, as in experiments 11 and 12, so as to cut off the circulation in a great measure, the hemorrhages appeared hardly appreciable to the naked eye. And as we have seen above, there was no extravasation at all when the blood was substituted by an artificial liquid, as in experiments 6 and 7.

Therefore, the hemorrhages become less marked in proportion to the interference with the circulation of the blood in the part.

#### CHAPTER XI.

#### GENERAL CONSIDERATIONS.

It seems desirable at the close of a research such as we here record to offer a few brief and general considerations in connection with some of the methods and plans pursued in parts of the work, to group some of the conclusions, and to bring together deductions which are necessarily scattered. A summary is also desirable that we may set forth succinctly the essential actions of venom so as to make clear the important differences in the toxic influences of globulins and peptones, to facilitate the application of what we have learned to the treatment of snake bite, and to indicate new lines of research in the most promising directions.

Our discovery of the existence of two distinct classes of poisons in venoms, that both are doubtlessly represented in all venoms, only differing in relative proportions and slightly in chemical and physiological properties, that they possess activities akin but yet readily distinguished, and that they are proteids and closely related to principles normally existing in mammalian blood, seems to us as of grave importance. Our methods, however, for the separation of the poisonous substances in venoms are open to improvement, because the processes are slow, and since possibly one of the poisons at least is injured. It does not seem from the results of our physiological studies with these poisons that any of them excepting the copper-venom-globulin have suffered, but that this has been affected seems probable from its altered solubility, its comparatively low toxic power, and its physiological peculiarities compared with the other globulins. Doubtless the ordinary methods for the separation of the globulins from other proteids in solution could be used to advantage, but how far successful they may prove in isolating the globulins from each other can only be determined by extended and careful investigation.

The plan we adopted in studying venoms and their active principles on the arterial pressure, pulse, and respiration is probably open to much criticism, but any other course seemed unavoidable. Instead of studying all venoms together as though they were absolutely identical compounds, although from different sources, and each of the active elements, as for instance the peptones, together as identical, it would doubtless have been preferable to have made a detailed investigation of each venom, and of each of the active principles of that specimen. But this course could not have been pursued satisfactorily because of the meagre supply of poison. It was then simply a question as to whether we would take a very limited number of experiments with each venom and each of its active principles, and base conclusions thereon, or study the actions of all pure venoms together, of all the water-

venom-globulins together, etc., and then form our conclusions. The latter course seemed preferable: first, because of the similarity in the actions of all pure venoms and of the ready interpretation of any differences, and of the resemblance in the actions of members of each of the classes of poisons; second, because in some of the actions such diverse factors are at work as to give apparently contradictory results, so that conclusions founded upon a very limited number of experiments would likely be more misleading than in the plan we adopted.

We summarize the following important points, deduced chiefly from our studies of Crotalus venom, to which are added a few comments:—

- 1. Venoms bear in some respects a strong resemblance to the saliva of other vertebrates.
- 2. The active principles of venom are contained in its liquid parts only. The solid constituents, such as we observed suspended in the poison, consist of epithelium cells, some minute rod-like animal organisms and micrococci, etc., which, when separated from the liquid fresh venom by means of filtration and well washed by water are harmless. Micrococci are constantly present in fresh venom, but have nothing to do with its virulence.
- 3. Venoms may be dried and preserved indefinitely in this condition with but very slight impairment of their toxicity. In solution in glycerine they will also probably keep for any length of time.
- 4. There probably exist in all venoms representatives of two classes of proteids, *globulins* and *peptones*, which constitute their toxic elements; the former may be represented by one or more distinct principles.
- 5. When venom is taken into the stomach in the intervals of digestion, enough of the poison may be absorbed to produce death, especially in the case of those venoms which contain a larger proportion of the more dialysable peptone; but during active digestion the venom undergoes alteration and is rendered harmless.
- 6. Potassic permanganate, ferric chloride in the form of the liquor or tincture, and tincture of iodine seem to be the most active and promising of the generally available local antidotes.
- 7. Venom exerts a powerful local effect upon the living tissues, and induces more rapid necrotic changes than any known organic substance. It causes ædema, swelling, attended with darkening of the parts by infiltration of incoagulable blood, breaking down of the tissues, putrefaction, and sloughing.
  - 8. It renders the blood incoagulable.
- 9. When brought in contact with a vascular tissue of a warm-blooded animal it produces such a change in the capillary bloodvessels that their walls are unable to resist the normal blood pressure, thus allowing the blood-corpuscles to escape into the tissues. These lesions are, however, not analogous to those of inflammation, since in the latter process it is principally the white blood-corpuscles which emigrate from the vessels, and the blood is highly coagulable, while here the blood exudes en masse and coagulates with difficulty, if at all. Free access of air (probably of oxygen) appears to lessen the virulent effects. The mesentery exposed to air, and on which the venom is merely brushed, endures the venom longer and in much larger quantity than when the poison is injected into the unopened and

uninjured peritoneal cavity, or when directly thrown into the blood. There may be here also a question of temperature and other conditions.

The following facts as elicited in these investigations seem to be sufficient to explain the mechanism of the hemorrhages: the blood pressure has been shown to play a most important part; a watery salt solution substituted for the blood does not extravasate, hence, blood seems to be necessary; there always occur molecular changes in the bloodyessel walls from the effect of venom. That blood pressure is an important factor has been established by the observation that the hemorrhages as a rule occur first in the capillaries which are immediately next to or nearest the large bloodvessels. The hemorrhages take place soonest where the force of the blood current is first felt and cannot be sufficiently resisted, and in no case do hemorrhages seem to originate from vessels with strong walls like the arterioles or veins. Cutting off the circulation of a part, as, for instance, by ligation of the vessels of the mesentery, destroys the blood pressure, and, as a consequence, the hemorrhages are so slight as scarcely to be seen by the naked eye though venom was freely applied. Finally, the colloid, softened, diffluent condition of the red corpuscles must inevitably facilitate extravasations. It is impossible to have seen numerous cases of venom poisoning without noting a variety of symptoms often abrupt or unexpected. These often are due, as Dr. Mitchell long since pointed out, to accidental hemorrhages into brain, kidney, and heart tissues. They explain much which might otherwise seem inscrutable, and serve sometimes to give a marked individuality of symptoms to cases which survive long.

- 10. Among the most remarkable effects of venom is that upon the red blood-corpuscles. These bodies undergo substantial modifications, *i. e.*, they lose their bi-concave shape, become spherical and softened, and fuse together into irregular masses acting like soft elastic colloid material. This jelly-like condition of the corpuscles is no doubt doubly important: in connection with the extravasation of the blood, and in its probable interference with the normal respiratory functions of the blood-cells.
- 11. The direct action of venom upon the nervous system save as concerns the paralysis of the respiratory centres is of but little importance.
- 12. The alterations in the pulse-rate are dependent chiefly upon two antagonistic factors which are active at the same time, the one tending to increase the rate and the other to diminish it. The former is found in the increased activity of the accelerator centres and the other in a direct action on the heart. When we have the action on the accelerator centres removed by isolation of the heart from any centric influence we almost invariably find a diminution of the heart beats. Occasionally after this operation the pulsations are increased, but this alteration is attended, as in the case of the diminution of the pulse, by feeble heart beats, and accordingly is but a manifestation in another way of a depressed condition of the heart.
- 13. The variations in arterial pressure are due chiefly to three causes, depression of the vaso-motor centres, depression of the heart, and irritation and consequent constriction or blocking up of the capillaries. It seems not improbable that all of these are consentaneously active, and it therefore follows that such alterations are dependent upon the relative degree of power exerted by any one of these factors. Our

results indicate that the profound primary fall of arterial pressure is chiefly due to depression of the vaso-motor centres and is in part cardiac, that the subsequent recovery is capillary, while the final fall is cardiac. The initial fall does not continue, because the constriction of the capillaries is, for a time at least, capable of compensating the depressed action of the central organ of circulation.

14. The respirations are primarily increased and secondarily diminished. Here again we have two antagonistic factors at work together, one tending to increase and the other to diminish the rate. The former is an irritation of the peripheries of the vagi nerves and the latter a depression of the respiratory centres; whether we have an increase followed by a decrease or a decrease from the first will depend upon the relative intensity of the action of the venom on these two parts. When the action of the venom is sufficient to profoundly depress the centres the excitation of the peripheries may prove futile.

15. Death in venom-poisoning may occur through paralysis of the respiratory centres, paralysis of the heart, hemorrhages in the medulla, or possibly through the inability of the profoundly altered red corpuscles to perform their functions. There can be no question, however, that the respiratory centres are the parts of the system most vulnerable to venom, and that death is commonly due to their paralysis.

A general survey of the chief physiological actions of venoms leads us to believe that the most important effects are upon the respiratory and circulatory apparatuses, and that in the production of these results antagonistic factors are at work so that we sometimes have observations which seem directly contradictory. When it is remembered that there are two classes of poisons in venoms, that each class possesses certain distinguishing physical, chemical, and physiological differences, although closely related, it is easy to conceive of the cause of the existence of antagonistic actions and the necessarily varying results.

A comparative study of the actions of the globulins and peptones indicates that the globulins produce swelling and blackening of the parts by infiltration of incoagulable blood; they are the more potent in producing ecchymoses, in destroying the coagulability of the blood, in modifying the red-corpuscles, and in the production of molecular changes in the capillary walls; their action on the accelerator centres of the heart is more notable than that of the peptone, hence they are more active in causing the increased pulse-rate; they exert, too, a more marked action on the vasomotor centres in producing the primary fall of pressure and are the greater depressants of the heart; they also act more powerfully upon the respiratory centres to paralyze them. The peptones are more active in the production of ædema, in the breaking down of the tissues, in the production of putrefaction and sloughing; they have little power to produce ecchymoses, to prevent coagulation or modify the capillary walls or the blood-corpuscles; they have less tendency to accelerate the pulse; they tend to increase the blood-pressure by irritating the capillaries, and are the principal factor in exciting the peripheries of the vagi nerves in the production of the increased respiration-rate.

A knowledge of these peculiarities in the actions of *globulins* and *peptones* coupled with the fact that the two classes exist in different proportions in the various species of venoms is of great importance in explaining the diverse pathological

appearances in cases of poisoning in different kinds of snake-bite—and suggests immediately the cause of the frightful local changes which are seen after the bite of the Crotalidæ but scarcely at all in Cobra-poisoning. It must not, however, be supposed that the peptones or globulins for instance are absolutely identical physiologically in every venom, as they are probably modified physiologically as well as chemically, although we do not doubt that on the whole the type of action is carried throughout all species. Cobra venom does not produce the marked lesions of Crotalus-poisoning because it is so lacking in globulins; it is weak in the production of the local swelling and blackening of the parts, of the ecchymoses, of the altered corpuscles and of the non-coagulability of the blood, but the effects of Cobra venom are closely in accord with the actions peculiar to peptones. The peptone of Cobra seems to have a more decided power in producing convulsions than that of the rattlesnake.

The fact that the active principles of venom are proteids, and closely related chemically to elements normally existing in the blood, renders almost hopeless the search for a chemical antidote which can prove available after the poison has reached the circulation, since it is obvious that we cannot expect to discover any substance which when placed in the blood will destroy the deadly principles of venom without inducing a similar destruction of vital components in the circulating fluid. The outlook then for an antidote for venom which may be available after the absorption of the poison lies clearly in the direction of a physiological antagonist, or, in other words, of a substance which will oppose the actions of venom upon the most vulnerable parts of the system. The activities of venoms are, however, manifested in such diverse ways and so profoundly and rapidly that it does not seem probable that we shall ever discover an agent which will be capable at the same time of acting efficiently in counteracting all the terrible energies of these poisons.

It is now most desirable that our discovery of the complex chemical nature of venoms should be made the groundwork in India of a study of the poison of the Bungarus, the Daboia, and especially of the dangerous Hydrophideæ. So far all efforts on our part to obtain the venoms of Australian and South American snakes have failed, so that these and the dreaded Vipère Fér-de-lance and the large Elaps of Mexico remain so far really unstudied.



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# DESCRIPTION OF PLATES.

#### PLATE I.

- Fig. 1.—Poisoning by venom peptone of Crotalus adamanteus. Local appearances on section after death.
- Fig. 2.—Poisoning by venom peptone of *Crotalus adamanteus*. Local appearances after death and before laying the part open. The ædematous prominent swelling is well shown, but is made rather too darkly red.
- Fig. 3.—Local effects of venom peptone, when the poisoning is chronic. The grayish semi-gangrenous muscles are shown in contrast with the uninjured muscle of the opposite side.

### PLATE II.

- Fig. 1.—Extensive local lesions after death from venom globulin (dialysis globulin). From Crotalus Adamanteus venom.
- Fig. 2.—Local lesions after death from a solution of dry Cobra venom—rabbit,
- Fig. 3.—Contrast with Fig. 2 the profound local change caused in a rabbit by venom of Crotalus. In both cases fatal results took place in two hours, the doses having been small.

### PLATE III.

- Figs. 1 and 2 exhibit the increased adhesiveness of human-blood globules when the fresh blood has been mixed with fresh venom.
- Fig. 3.—Naked-eye view of loop of mesentery in a cat showing effects of local application of venom of Crotalus. Extensive hemorrhages separate the two peritoneal layers, and are seen to have oozed through them freely.
- Fig. 4.—First microscopic appearances of hemorrhage from capillaries of mesentery of cat. Figs. 5, 6, 7.—Successive stages of increasing loss of blood.

#### PLATE IV.

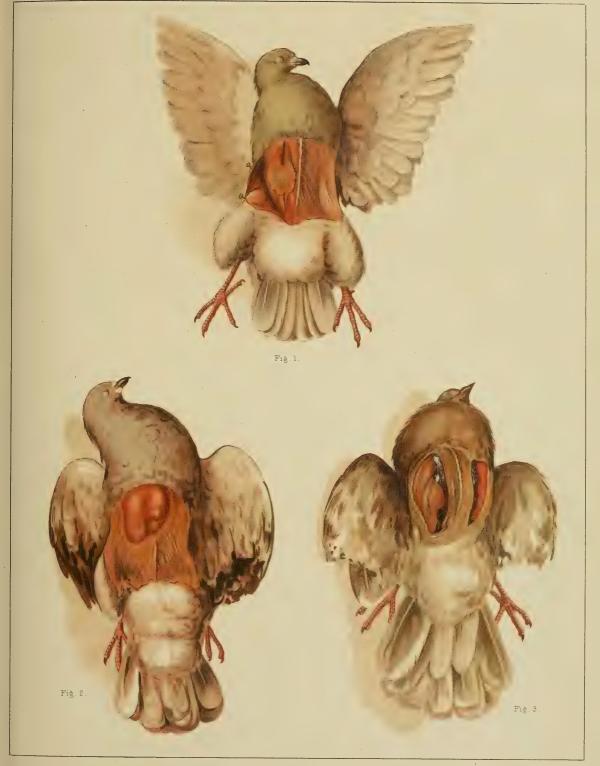
Microscopic appearances of human blood on being mixed with fresh venom. The alteration in form and the elasticity and adhesiveness are well shown in Fields 1, 2, and 3—Photographs by Dr. Geo. A. Piersol.

## PLATE V.

Extensive hemorrhagic lesions in abdominal organs of etherized rabbit poisoned by intra-peritoneal injection of venom of Crotalus adamanteus.

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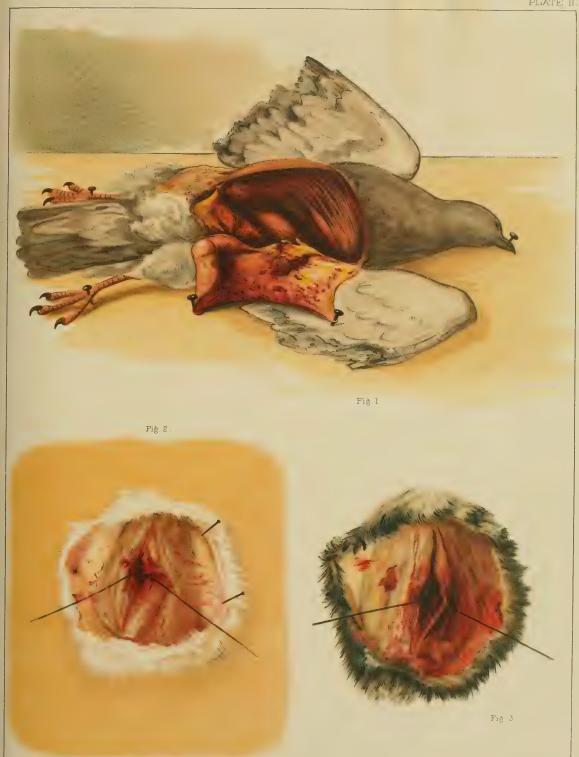










Fig. 1

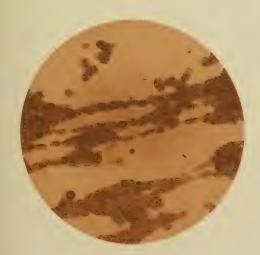


Fig 2.



Fig 3









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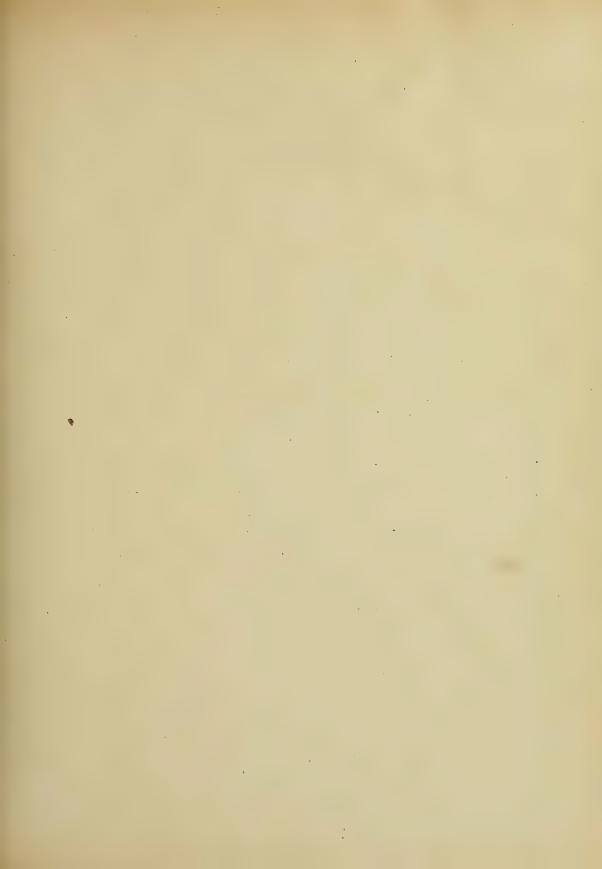
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# GENESIS

OF

# THE ARIETIDAE.

BY

ALPHEUS HYATT.

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1889.

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### ADVERTISEMENT.

The present work is published by the Smithsonian Institution in cooperation with the Museum of Comparative Zoology, Cambridge, Mass., the drawings for the plates having been made at the expense of that establishment.

This work has been recommended by Mr. Alexander Agassiz.

In accordance with the rule of the Institution, requiring the formal approval by selected experts of every Memoir offered for publication in the Smithsonian "Contributions to Knowledge," it was submitted for examination to Charles A. White and to William H. Dall; by whom it was also strongly commended, and it has been accordingly accepted for publication in the series of "Contributions."

S. P. LANGLEY,
Secretary Smithsonian Institution.

SMITHSONIAN INSTITUTION, WASHINGTON, D. C., February, 1889.

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## PREFACE.

I't is a common mistake to designate my classification as "embryological." It will be found by those who read these pages, that the whole life of the individual, and all its metamorphoses, have been deemed essential standards for the estimation of affinities. Even the degradational metamorphoses of old age are used as characteristics of value in the generic descriptions; it is properly speaking an ontological classification.

The researches were conducted almost wholly in Museums, because it was found impracticable to study stratigraphical superposition in the field. This part of the work has already been accurately done by local geologists, and my notes were largely made upon their collections. More extended studies might have made the work more accurate than it is, but this was not possible for me.

I desire to record my deep sense of obligation to the late Prof. Louis Agassiz, under whose direction my studies upon the Arietidæ were begun. His instruction and advice were none the less valuable because we differed in theoretical views; to him I owe the methods of observation which are used in all my work.

His son, Alexander Agassiz, has also laid scientific men in this country under heavy obligations, and this essay could not have been completed or published but for his sympathy, and for the liberal manner in which he has sustained by large personal sacrifices the collections and the cause of scientific research in the Museum of Comparative Zoölogy.

Professor Langley, Secretary of the Smithsonian Institution, has shown the greatest consideration and courtesy, and in undertaking the speedy publication of this memoir after the Museum of Comparative Zoölogy had been obliged for want of funds to postpone its issue indefinitely, has saved the results from becoming antiquated before they were made public.

My principal studies outside of this Museum were made in the Museum of Stuttgardt, and there I received unwearied attention and help from Prof. Oscar Fraas, and the use of superb collections. Professor Quenstedt of Tübingen gave me the benefit of much valuable information, and threw open his collections without reserve, and I am indebted for similar favors to Prof. Guido Sandberger at Würtzburg, Prof. Karl Zittel of the Museum at Munich, and to Professor Mösch at Zürich. The late M. Barrande, Professor Gaudry and his assistant Dr. Fischer of the Jardin des Plantes,

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Professor Hébert and his assistant M. Munier-Chalmas of the Sorbonne, Paris, were equally kind and liberal. I desire also to thank M. Collenot, M. Bréon, and Dr. Bochard, for 'their kind attention and the free use of the collections at Semur. Professor Owen and Dr. Henry Woodward of the British Museum, Mr. Etheridge of the Geological Museum, the authorities of the Bristol Museum, and Dr. Thomas Wright, gave me similar opportunities for study, and Mr. Marder at Lyme Regis assisted me in the field. Prof. Jules Marcou has materially aided the work by the loan of rare books not obtainable elsewhere, and I am also indebted to Prof. J. D. Whitney for similar loans from his library. Professor Emerson of Amherst has given me valuable information, and the use of his collection. I was unfortunate in finding the curators of collections either absent or sick at Hanover and Heidelberg; but in all practicable cases ample opportunities for study were given me, except at the Museum of York, England, where unvielding regulations prevented access to the interior of the cases, and my identifications there were consequently made without handling the specimens. I am also indebted to Professor Cope and Dr. John A. Ryder for the results of investigations which have thrown much light upon vexatious questions of theory, and which have not been properly represented by quotations in the text of this work, the general remarks having been necessarily cut down to the narrowest possible limits.

The essay on "Fossil Cephalopods in the Museum of Comparative Zoölogy" was written in large part as an introduction to this monograph, but for obvious reasons has not been used. The following conclusions, copied with some emendations and corrections from that essay, may be useful, however, in giving the reader a view of the theoretical opinions entertained by the author.

- 1. Law of Morphogenesis.—We have endeavored to demonstrate that a natural classification may be made by means of a system of analysis in which the individual is the unit of comparison, because its life in all its phases, morphological and physiological, healthy or pathological, embryo, larva, adolescent, adult, and old (ontogeny), correlates with the morphological and physiological history of the group to which it belongs (phylogeny).
- 2. Organic Equivalence. All new characteristics, even those which are purely mechanical reactions of the tissues, arise in a similar manner, as reactions due to the exciting agency of the more general or more localized physical causes. They are therefore necessarily, and because of this mode of origin, the corresponding organic, or suitable complementary equivalents of these physical causes, both structurally and functionally.
- 3. After their origin, however, and during their subsequent history, organic equivalents or characteristics are divisible into two categories: those which become morphological equivalents, and are essentially similar in distinct series, and those which are essentially different in distinct series, and may be classed as morphological differentials.
- 4. Morphological Equivalence.—In the different genetic series of a type derived from one ancestral stock there is a perpetual recurrence of similar forms in similar succession, which are usually called representative and often falsely classified together, though they really belong to divergent, genetic series.

<sup>&</sup>lt;sup>1</sup> Proc. Am. Ass. Adv. Sci., XXXII., 1883.

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5. These forms and their similar characteristics are not derived by direct inheritance from the common ancestor, in which all the forms are necessarily similar and primitive, but originate everywhere independently of hereditary influences in the different series, and also in all formations independently of chronological or chorological distribution.

- 6. This evolution of similar morphological changes in the forms of different genetic series must be regarded as the similar reactions or efforts of a common organism in direct response to similar generally distributed physical causes active in the same habitat, and are therefore necessarily similar to each other, though in different genetic series. As a whole, they may be said to express the general tendencies of modification, due to the efforts of the common-radical and common organization while spreading in all directions and in different genetic lines to respond to similar physical causes, and meet their requirements with suitable changes. They are, therefore, structural equivalents of each other in different series, and functional equivalents of the general requirements of the environment or habitat, or, in other words, purely physical selections.
- 7. Morphological Difference. Differentials are absent in the first members of series, on first appearance in their descendants transient, but afterwards tend to become invariable, or fixed in the stock or series, being perpetuated by direct inheritance in successive generations, species, etc. They finally often disappear in the retrogressive or highest and last occurring members of each series, or in aberrant forms when on the same level.

8. They have no determinate mode of succession, but are usually more or less isolated modifications, and arise first in individuals or varieties, but afterwards become characteristic of species, and finally of the major part of the direct line in species, or descendent series.

- 9. They are, therefore, strictly adaptive, variable characteristics, and not directed in their occurrence or development by any more or less invariable law of successive modification, as are the morphological equivalents. We have failed in finding any differentials of great importance whose prepotence as hereditary characteristics could not be accounted for by the law of use and disuse in connection with habits. The differentials of small series, species, genera, and families, which we have not been able to analyze thoroughly, may be due to the action and reaction of individual animals upon each other, or, in other words, to natural selection.
- 10. Differentials, therefore, can be separated from other characteristics of the same parts by careful observation and close analysis of their behavior in series, but cannot be specifically predicted from the study of other series; whereas, morphological equivalents can be predicted with the same certainty as the recurrence of cycles in physical phenomena. Thus we can say of any new series of Nautiloids or Ammonoids, that, the habitat remaining similar, they will, whenever or wherever found, tend to develop arcuate, coiled, close-coiled, or discoidal and finally involute forms in progressive series, and reverse this process in retrogressive series.
- 11. Acceleration in Development.—All modifications and variations in progressive series tend to appear first in the adolescent or adult stages of growth, and then to be inherited in successive descendants at earlier and earlier stages according to the law of acceleration, until they either become embryonic, or are crowded out of the organization, and replaced in the development by characteristics of later origin.
- 12. Geratology. Modifications which tend to appear in the old age of the individual of progressive series correlate with the modifications taking place in pathological series of all grades, and in geratologous and retrogressive forms of all kinds, however progressive they may be in certain characteristics. Geratologous forms, therefore, show that the development of retrogressive characters has been stimulated so as to take the place of the hereditary progressive, thus either partially or completely replacing them. Partial replacement is often accompanied by the early development of hereditary progressive characteristics.

- 13. Acceleration in Degeneration. Geratologous forms may, therefore, be the highest members of progressive series, or the terminal members of retrogressive series, and the stimulation of the development appears to take effect upon both progressive and retrogressive characteristics; thus producing, at the same time and in the same animal, first, the earlier development of some of the progressive characteristics combined with geratologous characteristics; secondly, the earlier development of geratologous characteristics and their fusion with larval characteristics, which occasions the complete replacement of progressive characters, and occurs only in the extreme forms of retrogressive series, and in parasites.
- 14. The law of acceleration in development seems, therefore, to express an invariable mode of action of heredity, in the earlier reproduction of hereditary characteristics of all kinds, and under all conditions. In progressive series it acts upon healthy characteristics, and appears to be an adaptation to favorable surroundings, and in retrogressive series upon pathological characteristics, and is probably an adaptation to unfavorable surroundings, usually leading to the extinction of the series or type.
- 15. The Three Phases of Development.—In following up series, it has been found that the development of ancestral forms is simple and direct (Epacme); that of their more specialized descendants becomes gradually indirect (Acme), acquiring complicated intermediate or larval stages; and that of the terminal retrogressive or geratologous and pathological forms becomes again more or less direct (Paracme.)
- 16. The introduction of adaptive larval stages into the history of individual development in any series appears to be due to the direct exciting action of the surroundings, and their absence or subsequent suppression to some physical agency, changes of habit, or protection, or pathological causes. All of these causes must, however, be considered as similar in their effect upon the young. They are stimulants, producing acceleration or excessively rapid development of the ancestral progressive characteristics, or of the retrogressive, or primitive larval characteristics inherited from the progressive forms.
- 17. This agreement in the mode of development of the individual according to its position in the history of the group completes the correlations which exist between the history of the individual (ontogeny) and the history of the group to which it belongs (phylogeny). Using Haeckel's nomenclature, the three periods of ontogenesis, Anaplasis, Metaplasis, and Cataplasis, correlate with the three periods of phylogenesis, Epacme, Acme, and Paracme. In addition to this general correlation, we now find that during the epacme of a group the development of individuals is anaplastic or progressively direct; during the acme of a group, metaplastic or progressively indirect; and during the paracme of a group, cataplastic, or retrogressively direct. We have also found, that, in the history even of small groups, the epacme, acme, and paracme may often succeed one another in geologic time, and show similar correlations, so that we can often distinguish epacmic faunas, acmic faunas, and paracmic faunas in chronological succession. In series, also, epacmic forms, acmic forms, and paracmic forms, either in series of species or varieties, may occur in geological succession in different faunas, or in zoölogical gradation in the same fauna.
- 18. Law of Variation.—The action of physical changes takes effect upon an irritable, plastic organism, which necessarily responds to external stimulant by an internal reaction or effort. This action from within upon the parts of organisms modifies their hereditary forms by the production of new growths or changes, which are, therefore, adapted or suitable to the conditions of the habitat, and are therefore physiologically and organically equivalent to the physical agents and forces from which they directly or indirectly originated. In so far, then, as causes and habits are similar, they probably produce representation or morphological equivalence in different series of the same type in similar habitats; and in so far as they are different, they probably produce the differentials which distinguish series and groups from each other.

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19. The radical and epacmic forms of the Arietidæ probably originated in the Northeastern Alps, and migrated from thence southerly and westerly into Italy, and also in another direction westerly into South Germany and the Côte-d'Or. In these last two faunas new series of acmic forms arose by modification, and these and the paraemic forms which seem to have arisen in the same basins flowed back into the Northeastern Alps, and thence into Italy, during Bucklandian and later times. They were also distributed from these two basins to all others to the north and south of them in Central Europe. The Northeastern Alps and the South German and Côte-d'Or basins constitute a Zone of Autochthones for the Arietidæ, and other faunas to the north and south of these are what we have called Residual Faunas.

The materials in the Museum of Comparative Zoölogy consist of various collections made in England by Damon, Marder, and Wright; Boucault's famous collection from the Côte-d'Or, containing several of D'Orbigny's types, and in part named by him, or by direct comparison with his collection; a special and very large general collection, especially rich, however, in South German species, purchased from Dr. Krantz; a valuable exchange from the Museum at Stuttgardt named by Professor Fraas; Professor Bronn's collection labelled by him; a number of valuable species, principally from Belgium, from L. de Koninck's collection; a similar lot presented by Prof. J. Marcou, from various localities in Europe; and others not sufficiently important to be mentioned here.

ALPHEUS HYATT.

Cambridge, April, 1889.



# GENESIS OF THE ARIETIDÆ.

I.

#### INTRODUCTION.

ORIGIN AND CHARACTERISTICS OF SUBORDERS.

THE succession of forms among the silurian members of the genus Mimoceras indicates that true gyroceran shells occurred among Ammonoidea, differing from the similar forms among Nautiloids only in the possession of a globular protoconch and a small ventral lobe. In some silurian and devonian Anarcestes these permanent adult stages are repeated in the development of the young. Those in Mimoceras compressum are truly cyrtoceran, or open curves at first; and in others, as in a variety of Anarcestes feeundus described by Barrande, they are straight.

The next stage of growth is a loose-coiled or gyroceran form, like the adult of Mimoceras. These stages can only be accounted for as hereditary tendencies of growth in a type which is being rapidly changed from a primitive ancestral straight form with simple sutures into a close-coiled nautilian shell,<sup>1</sup>

Branco<sup>2</sup> describes and figures a specimen of Bactrites with a protoconch similar to the very peculiar ovoid protoconch of Mim. compressum. He quotes Beyrich, who gave him this specimen, as authority for the view that Bactrites is connected with Mimoceras as Baculites is with the normal Ammonoids of the Cretaceous. This idea was first published by Quenstedt in his "Die Cephalopoden," and it is quite possible that Bactrites of the Devonian may be a degraded form of Mimoceras, but in that case the latter is also a degraded form of Anarcestes, or transitional between it and Bactrites. To establish this proposition, forms of Mimoceras and Anarcestes should be produced in which uncoiling occurred in adults after a close-coiled stage of growth had been passed through. Such degraded forms are common in the Jura and Cretaceous, and enable the observer to connect Baculites with the normal coiled Ammonoids of the same formations. Whether this be so or not, the straight Bactrites-like young of some forms of Anarcestes, the gyroceran young of others of the Goniatitine, and the gyroceran adults and young of Mimoceras, indicate the derivation of Goniatitinæ to have been from silurian straight shells similar to Bactrites, if not directly from that genus itself.

<sup>&</sup>lt;sup>1</sup> Genera Foss. Ceph., pp. 303, 304, 309, Proc. Bost. Soc. Nat. Hist., XXII., 1883.

<sup>&</sup>lt;sup>2</sup> Zeitsch, Deutsch, Geol. Gesell., XXXVII. p. 1.

We pointed out in "Embryology of Fossil Cephalopods," that the loosely coiled stages prevalent among Nautilinidæ were repeated in the early stages of development in some of the Goniatitinæ and in the later Ammonoids. This repetition was indicated by the form of the embryo which was flattened and depressed, and also in the first sutures and in the embryonal umbilici. These last are two conical or flattened depressions on either side of the protoconch, at its junction with the apex of the conch. They were accounted for as remnants of the umbilical perforation found in the young and adults of Mimoceras and all coiled Nautiloids.

In our "Genera of Fossil Cephalopods" we narrowed this generalization by comparing the first whorl of the embryo in the close-coiled Goniatitinæ and in all Ammonitinæ with Anarcestes, thus bringing the affinities of all the Ammonoidea to a focus in the silurian genus Anarcestes. These and other similar observations, published before and since the work quoted above, have been founded upon the law of acceleration formulated also in the Preface of this monograph, pp. v, vi, Art. 11 and 14.

Dr. Branco's extensive and accurate researches have shown that all of these opinions, though founded upon a few specimens only, were sound, and that the law of acceleration can be relied upon as a working hypothesis. Though treating us otherwise with more than just appreciation, this author failed to notice that we had used the law of acceleration in development, or made our inductions with the view of demonstrating its truth as a working hypothesis, and consequently attributed the discovery of this law to Würtenberger.

Among Nautiloids the straight shells in each series appeared first; they were succeeded by the cyrtoceran, gyroceran, and close-coiled. Among Ammonoids there is only one series - Bactrites, Mimoceras, and Anarcestes - which is parallel with any one series of the many occurring among Nautiloids. The open-whorled stages of the young of Anarcestes and other Goniatitinæ represent a transitional and highly accelerated development. This transitional character is also indicated by the fact that, except in Mimoceras and some species of Anarcestes, the occurrence of the gyroceran form, even in the young, is sporadic. It occurs, as demonstrated by Barrande, in one variety of Gymniles fecundus, and not in the other. Sandberger has shown similar though less marked variations in the young of Anar. subnautilinus, and Branco has described the embryo of var. vittiger of the same species as close-coiled. Other examples might be given, but it only remains to notice Branco's doubts of the accuracy of our drawings of the young of Gon. atratus and Gon. Listeri. Both of these were found by him to belong to his close-coiled division of the Asellati of the Carboniferous. Our drawings were made with a camera. The details they contain show, better than any defence we can make, that they were also closely studied by the author, and often corrected before being placed upon stone. They indicate that primitive gyroceran forms of young are occasionally found even among the highest forms of carboniferous Goniatitinæ.

<sup>2</sup> Paleontogr., 1880, 1881, XXVI., XXVII.

<sup>&</sup>lt;sup>1</sup> See especially articles "Whorls" and "Umbilicus," Bull. Mus. Comp. Zoöl., III. No. 5.

The depressed semi-lunar whorl appears first in the adults of Anarcestes. It is subsequently found in the young as a stage immediately succeeding the more cylindrical whorl of the gyroceran stage, when that occurs. In very close-coiled forms, the latter may be omitted, or be only slightly indicated, and then the anarcestian whorl appears at the beginning of the apex. In fact, this tendency in Latisellati, and especially in Angustisellati, affects the shape of the protoconch which is excessively depressed in the embryos of the higher suborders.

We have, therefore, considered it convenient to designate the anarcestian form of whorl as the primary radical of the Ammonoidea, reserving the terms primitive and transitional radicals for the straight and gyroceran modifications as they appear in Bactrites and Mimoceras.

The different series of the Clymeninæ and Goniatitinæ, and the Arcestinæ, often begin with, and maintain persistently in full-grown shells, the primary radical form. The Ceratitinæ, Lytoceratinæ, and Ammonitinæ, on the contrary, have this depressed form but rarely, except in their protoconchial stage,—and at the beginning of the apex or true conch, while it remains in what we have called the goniatitic stage of development.

The Clymenine of the Devonian begin, when zoologically arranged, with discoidal forms having depressed semi-lunar anarcestian whorls. These depressed whorls are exchanged in the higher forms for compressed discoidal whorls, and these in turn for compressed involute whorls. The suborder includes several genera and in each there occur examples of this mode of succession, or rather procession, of forms, forming parallel series.<sup>1</sup>

The sutures of the genera Beneckia, Longobardites, Lecanites, Norites, Meekoceras, Hungarites, and Carnites show them to be true Ceratitine. We should, with our present information, be disposed to include these, and all the genera mentioned by Mojsisovics as belonging to his group of Ammonites trachyostraca, in the Ceratitine, distinguishing them by their well-known and peculiar sutures from the Arcestine, Ammonitine, and Goniatitine.

The more or less compressed whorl, which in section can be described as helmet-shaped, is the natural successor of the depressed anarcestian whorl both in the growth of individuals and in the evolution of series of species. We have considered this in the work quoted, therefore, as the secondary radical.

The secondary radicals 2 are prevalent in the Ceratitinæ, as shown by the extensive researches of Mojsisovics in the remarkable and masterly treatise above quoted. They completely replace the primary radicals as generators of series in the Trias, except in the paleozoic survivors of the suborder Arcestinæ. So far as the sutures are concerned, however, the Ceratitinæ, though distinctly characteristic of the triassic faunæ, are like the Goniatitinæ. The young of Longobardites is really a Goniatite, similar to Prolecanites.

<sup>&</sup>lt;sup>1</sup> Genera of Fossil Cephalopods, Proc. Bost. Soc. Nat. Hist., XXII. p. 312.

<sup>&</sup>lt;sup>2</sup> We formerly included (Gen. Foss. Ceph., p. 324) in secondary radicals some quadragonal whorls like those of the adults of Xenodiscus; but we are now disposed to consider this an error, arising from not having observed that the young of these forms often possessed, during earlier stages of growth, the secondary or helmet-shaped whorl. This evidence shows that, in the most ancient periods as well as in later times, quadragonal whorls were derivative modifications of the compressed helmet-shaped secondary radicals.

Norites is considered by Mojsisovics as allied to Pronorites, a genus of Goniatitinæ, and by Griesbach, Zittel, and the author as allied more nearly to another genus of the same suborder, Sageceras. Throughout the group the lobes and saddles form a simple series in which very little differentiation is observable except in the highest forms. The ventral lobe is very broad and short, and the siphonal saddle broad and shallow. The survival of prolecanitian characters in these outlines is apparent the moment we dispense with the denticulations of the lobes and reduce the sutures to their primitive outlines. The Arcestinæ of the Dyas are known only by one species, described by Waagen, Cyclolobus Oldhami, which has whorls of the anarcestian shape. It is an involute species, and there may be others of this genus in the same formation, not yet discovered, which have more discoidal whorls.

According to our mode of translating the affinities of the forms, they arrange themselves as follows. Popanoceras of the Dyas, as the direct descendant of Prolecanites, inherits the tendency to have lobes and saddles of very nearly the same size, with lobes having trifid or bifid terminations similar to those of the young of Monophyllites, and also transitional to the sutures of the dyassic Cyclolobus, the most ancient of the true Arcestine. If we are right, the young of this last form, when examined, will be found to be similar to *Popanoceras antiquum* at a stage when its sutures have not yet acquired marginal lobes.

The siphonal saddle in these forms and in true Arcestine is small, often attenuated, and the ventral lobe large and often broad. The remaining lobes and saddles are more nearly of the same size, numerous, and formed a gradually lessening series inclining towards the umbilicus. The same aspect is common in the simpler shells of Megaphyllites and Monophyllites, but in these the large phylliform saddles, with entire outlines at their bases, exhibit closer approach to the Prolecanitide. Arcestine, therefore, retain in their sutures the proportions of paleozoic forms of Goniatitine which have numerous lobes, but depart from them in having more complicated and ornate marginal digitations. The series, with some exceptions, have involved whorls which can only be considered as parallel with the more involute shells of silurian and devonian Anarcestes. With respect to its forms and the smoothness of the shell this series is a survival of purely paleozoic modifications.

The Lytoceratinæ form a separate phylum, distinguished usually by the absence of true pilæ (ribs), the larval form and characteristics of the adult shell, and the leaf-shaped marginal saddles of the sutures. Lytoceras, in its smooth or unpilated shell, rounded abdomen, peculiar siphonal saddle, and phylliform marginal saddles, appears to be a more progressive form of the same genetic series as Megaphyllites and Monophyllites of the Trias. Even the peculiar coarse striations of the shells of these genera are often repeated among the Lytoceratinæ of the Jura.

Megaphyllites of the Trias is evidently closely allied to Monophyllites. The siphonal saddle is similar to that of Monophyllites, and the marginal

 $<sup>^1</sup>$   $Arcestes\ priscus,$  Waagen, is probably also a species of Cyclolobus. Geol. Surv. Ind., Salt Rauge, ser. 13, I. i, pl. ii. fig. 6.

saddles are phylliform. The young of *Monophyllites Suessi*, Moj.,¹ of the Trias, has sutures similar to the adults of *Popanocerus antiquum*² and *Kingianum* of the Dyas,³ which are true Goniatitinæ. The sutures of Popanoceras are in their turn transitional between Monophyllites and the more normal Goniatitinæ of the genus Prolecanites.

Triassic Ammonoidea have shallow ventral lobes and very prominent broad siphonal saddles, thus giving the first lateral saddles the aspect of being adjuncts of the siphonal saddle. In consequence of the more direct descent of Lytoceratinæ of the Jura from primitive forms, their sutures persist in retaining triassic outlines, having usually short abdominal lobes, large siphonal saddles, with the superior laterals apparently set upon their sides, the larger lobes expanded and profusely branching at the top, the saddles expanded and profusely branching at the base, the auxiliary lobes and saddles more numerous and more nearly equal to the larger lobes and saddles than in Ammonitinæ. Neumayer has demonstrated trumpet-like apertures in Lyt. immane.<sup>4</sup> The frilled and elevated ridges in shells of many forms indicate that these are perhaps not uncommon in this group.<sup>5</sup>

The normal forms of the Ammonitine, the Arietidæ of the Lower Lias, can be united to the genus Gymnites through Psiloceras. Gymnites can be traced back to the Goniatitinæ through Arcestes of the Trias and Cyclolobus of the Dyas. The Ammonitinæ do not, therefore, come directly from the Goniatitinæ, as do the Lytoceratinæ, but are probably direct offshoots of the lower Arcestinæ. The Ammonitinæ include not only the typical jurassic and cretaceous forms, but also the allied radical genera Schlotheimia and Psiloceras of the Lias, and Gymnites and Ptychites of the Trias.<sup>6</sup>

In Gymnites of the Trias, the primary radical is exchanged for the more compressed discoidal secondary radical, but still smooth shell, which is also characteristic of Psiloceras of the Lias. The sutures are correlatively modified, and begin to assume the aspect and proportions of the true Ammonitinæ. The siphonal saddle is more prominent, but still retains in many species the pointed aspect derived from the Goniatitinæ. The narrow first lateral saddles are apt to appear like adjuncts of the siphonal saddle, owing to the great size and breadth

- <sup>1</sup> Mediterr. Triasprov., pl. lxxix. fig. 4 a-e.
- Arcestes antiquus, Waagen, Salt Range, Pal. Ind., ser. 13, I. i, pl. i. fig. 10.
- <sup>3</sup> Russia and Ural, M. V. K., II. pl. xxvii. fig. 5.
- <sup>4</sup> Mojsis. et Neum., Beitr., III., 1883, 1884, pl. xx.
- <sup>5</sup> Schlönbach, Paleontogr., XIII. p. 169, pl. xxvii. fig. 3, describes Amm. hircicornis, one of the Lytoceratine, having a series of prominent flaring ridges indicating permanent apertures of similar form. The slight, blunt rostrum is a notable characteristic of these apertures. Unfortunately, very few have been preserved, possibly owing to the fact that they were in most species, as in the two mentioned, thin flaring ridges, easily destroyed. We can only suggest, therefore, that this form of rostrum night have been peculiar to this suborder.
- <sup>6</sup> In "Genera of Fossil Cephalopods," in 1883, we expressed this opinion as follows: "This genus (Cyclolobus) is very important, since it enables us to show the gradations by which the Prolecanitida approximate to Arcestes, Ptychites, and Monophyllites." Mojsisovics, with new materials from Spitzbergen, has lately demonstrated the correctness of this opinion in part, and gives conclusive evidence of the probable derivation of Arcestes and Ptychites from Popanoceras. Arkt. Trias Fauna, Mem. Akad. St. Petersb., XXXIII. No. 6, p. 66, pl. xv.

of the first lateral lobes and the shortness of the ventral lobe. The aspect of the second laterals in many species, and the gradation from these into the auxiliary lobes, show that they retain the more primitive aspect of the earlier forms in this part of the sutures.

Ptychites of the Trias has sutures similar to those of Gymnites, and the modified aspect of marginal lobes and saddles in both genera shows that, in spite of a near approach or resemblance in the sutures to many Lytoceratine, they cannot be considered as so nearly related to them as to Cyclolobus.

Mojsisovics says that the evidence of genetic connection of *Psiloceras planorbe* and *Gymnites incultus* rests alone upon the resemblances of the auxiliary lobes and saddles, and that the resemblances in form only occur between the discoidal Gymnites and the most involute Psiloceratites, the former being indeed much more involute than the most involute of the Psiloceratites. The genus Halorites of the Trias is regarded by Mojsisovics as the probable ancestor of the Arietidæ.

We cannot recognize that there are any very marked differences in the amount of involution or form between Gym. incultus and Gym. Palmai when compared with Psil. planorbe, and the resemblances of the sutures are exceedingly close, especially when the species of Psiloceras of the Mediterranean province are studied. The aspect of the shells in the three former are very similar, while in the types of Halorites already cited by Mojsisovics, Hal. Ramsaueri, semiplicatus, decrescens, and semiglobosus, they are very distinct. The range of form in Halorites embraces highly sculptured shells, altogether triassic in aspect. Neumayr's 2 and Wähner's 3 researches entirely confirm the position here taken and show that Psiloceras possessed a series of involute shells. Psiloceras and Gymnites, therefore, appear to be two parallel genera of the same group, in each of which discoidal forms give rise to more involute shells. Gym. incultus may be traced into the more involute Gym. Humboldti, and the still more involute Gym. Credneri. The adolescent young of Gym. Palmai, Mojsis. 4 and incultus 5 show less involution than the adult, and we may confidently expect that some correspondingly still less involute discoidal ancestral forms will be found. Mojsisovics has not yet published his observations in full, and his evidence is therefore not completed; but, so far as we now know, the derivation of Psiloceras seems to have been from Gymnites as a common ancestor and not from any forms of the Ceratitinæ like Halorites or its allies.

Mojsisovics has said, that out of his group of Ammonites leiostraca the genus Phylloceras alone persists and is but little changed in the Jura; whereas the Amm. trachyostraca, or Ceratitinæ, are more largely perpetuated, though much changed, in the true Ammonitinæ. Our view differs, since we consider all groups of the Trias to have been discontinued in the Jura except the Lytoceratinæ. It is probable that a close affinity existed between Psiloceras and Gymnites, and the former is a modified Triassic survivor in the Lias; but the constant reappearance of the psiloceran form in the young of undoubted Arietian

<sup>&</sup>lt;sup>1</sup> Amm. Gattungen, Verhand. Geol. Reichs., 1879, No. 7.

<sup>&</sup>lt;sup>2</sup> Unterst. Lias, Abhandl., Geol. Reich., VII. Unt. Lias, Mojsis. et Neum, Beitr., III.

<sup>&</sup>lt;sup>4</sup> Med. Triasprov., pl. lvii. fig. 2.

<sup>&</sup>lt;sup>5</sup> Ibid., pl. liv. fig. 3.

species shows that we must reckon it among the Arietidæ. The genus Schlotheimia is also a purely jurassic series, though undoubtedly triassic in respect to its sutures. The young of Schlotheimia catenata is an almost exact reproduction of the form described by Mojsisovics as Ægoceras Buonarotti in "Jahrbuch Geologischen Reichsanstalt," and afterwards referred to Celtites in his "Mediterranean Triasprovinz." The pilæ cross the whorls on the abdomen in the same way, and the general aspect of this discoidal shell is similar. It seems quite likely that this is a young shell of some species, and until its exact affinities can be determined it is of no great value. At present it would be difficult to say with any certainty to what genus it might be referred. Mojsisovics was evidently in doubt, since he states that it may be a young form of some species of Balatonites. The resemblance to the young of Schlot. catenata may be due to a purely pathological deformation, since the crossing of the abdomen by the pilæ occurs from disease in many species of the Arietidæ and other keeled groups of the Jura, notwithstanding the fact that it is normal in others. These facts, and the gradations of form between Schlotheimia and Psiloceras presented by the genus Wæhneroceras,3 and by the young of this last genus, lead us to think that Schlotheimia was derived from Psiloceras. The Ammonitina of the Jura, so far as known, show no special traces of their prolecantian descent, except in the discoidal shells and phylliform sutures of the genera just mentioned, and in the embryonic and generalized goniatitic characters of the apical stages of the shell. The ventral lobe of the Ammonitinæ is deep and narrow, the siphonal saddle small but more or less dentated by marginal lobes and saddles. The lateral saddles are broad and not so deeply divided by marginal lobes as in the Lytoceratine, the lobes are narrower at the tops than in that suborder, and the saddles consequently narrower at their bases. The great size and small number of the lobes is also a marked peculiarity. The superior lateral saddles and lobes are especially remarkable for size, and the auxiliary lobes and saddles much less important and more unequal as compared with the lateral lobes and saddles than in Lytoceratine. The marginal lobes and saddles are as a rule short and pointed, and the saddles rounded, but not phylliform. Possibly another distinction will eventually be demonstrated in the more constricted and rostrated apertures of many of the Ammonitine. The characteristics of the embryos and of the earliest stages do not yet seem sufficiently well known to be used in this connection.

The Ammonoids, therefore, according to our views, are not divisible into two grand divisions, but have six suborders: the Goniatitinæ, of the Silurian, Devonian, Carboniferous, Dyas, and Trias; the Clymeninæ of the Devonian; the Arcestinæ of the Dyas and Trias; the Ceratitinæ of the Dyas and Trias; the Lytoceratinæ of the Trias, Jura, and Cretaceous; and the Ammonitinæ of the Trias, Jura, and Cretaceous.

Unfortunately, there is not space enough within the necessary limits of this monograph to discuss the classifications of Mojsisovics, Fischer, and Zittel,

Vol. XIX., 1869, pl. xv.

<sup>&</sup>lt;sup>3</sup> A new genus described in this memoir.

<sup>&</sup>lt;sup>2</sup> Page 129, pl. xxix.

and the embryological divisions proposed by Branco.¹ The classification given above was necessary in order to introduce our remarks upon the Ammonitine, and show clearly why wé limited this suborder as defined above; any further discussion would lead us too far away from the immediate objects of this memoir.

#### NOMENCLATURE OF STAGES OF GROWTH AND DECLINE.

In a paper read before the Boston Society of Natural History, November 16, 1887, the author discussed the classification of the stages of growth and decline, dividing them as follows:—

- 1. The earlier stages, embracing the ovum (monoplast, Lankester), the monoplacula, and the diploplacula, were considered under one term, Protembryo, because of their parallelisms with the single and colonial Protozoa.
- 2. The next, or blastula stages, were classified under the head of Mesembryo, on account of their resemblances to the Mesozoa; the latter being those forms usually included in the sub-kingdom of Protozoa, but which have true ova and spermatozoa, and can be therefore separated as one-layered, spherical Blastrea, closely parallel with the blastula, and precisely intermediate between Protozoa and Metazoa.
- 3. The gastrula stages were considered as referable to true Metazoa, and were styled accordingly the Metembryo.
- 4. The earlier planula or ciliated stages were regarded as indicating a still very remote ancestral type, in common with Semper, Lankester, and Balfour, and were termed the Neoembryo.
- 5. The later ciliated stages—those which show the essential characters of the type to which the embryos belong—were classified as the Typembryo; ex. the veliger, nauplius, etc. The typembryos were considered as the last of embryonic stages, and those which followed were regarded as true larvæ on account of their more demonstrable connections with well known forms. It was found by applying this classification to the fossil Cephalopoda that the protoconch of Owen was the shell of a univalve typembryo, which must have been a veliger not very widely removed in structure from the similar shells of the embryos of Gasteropoda and Pteropoda.<sup>2</sup>

The principal difficulty of the application of this view lies in bringing the wrinkled and curious forms which occur upon the apices of some Nautiloids into

<sup>1</sup> Mojsisovics, Med. Triasprovinz; Fischer, Manuel de Conchyliologie; Zittel, Handbuch der Paleontologie; Branco, Paleontogr., XXVII., XXVII.

<sup>&</sup>lt;sup>2</sup> Robert Tracy Jackson, a pupil of the author, in an essay now in preparation ("Phylogeny of the Pelycypoda"), shows that the typembryo stage of mollusks is limited to an early period characterized by the existence of a shell-gland and the plate-like beginnings of a shell. Later veliger stages, he says, are referable to the class or phylum of Mollusca, to which the embryo really belongs, and he names them "Phylembryo" stages. The "prodissoconch" is a name given by Jackson to the embryonic, bivalvular shell of Pelycypoda, which is the equivalent of the protoconch of cephalous mollusca. The completed protoconch of the cephalous mollusca, and prodissoconch of Pelycypoda, Jackson considers as a stage later than that at which the phylembryonic characters are emphasized, and as the close of the embryonic shell period. His paper will give types of these and other stages considered in the several classes of mollusks.

exact relations with the indubitable protoconchs occurring upon the apices of the conchs of Ammonoids and Belemnoids. The wrinkled lump above referred to is unquestionably a part of the shell. It is not only closely attached, but the longitudinal striæ of the apex of the true conch are continuous upon the proximate parts of the lump. It had an aperture which must have remained open until the body of the veliger had entirely left the interior of the protoconch, and was then closed by the apical plate. There is a cicatrix upon the apex of the conch, which is invariably concealed by the lump when it is present, and in some examples we observed the fracture of the outer layer of the shell on the apex of the conch and outside of the ordinary boundary of the cicatrix, which could only have been caused by the violent removal of the lump. The wrinkled and contracted aspect of the lump when preserved can be accounted for by assuming it to have been composed of conchiolin. This also accounts for its almost invariable absence, since such an organ must have been easily lost or destroyed. The lumps must consequently be regarded as the remnants of conchiolinous protoconchs having elongated and narrow apertures; but probably they were, when in a living condition, much larger and more oval, and more similar to the protoconch of the Ammonoids. The continuity of the striæ from the conch to the protoconch also shows that the conch was built out from the aperture of the protoconch, layer after layer, and the concentric markings, and form of the apex, which correlates with that of the scar, sustain this idea. The figures on the following pages are less perfect than several other examples studied by the author since these were drawn. They do not show the passage of the external longitudinal striæ from the apex of the conch on to the surface of the protoconch.

A living chamber among recent and fossil Nautiloids marked a period of rest after a stage of growth. The septum, therefore, was not built until the animal arrived near the final steps, or had altogether stopped building out the sides of that part of the shell in which it lived. At any rate, we can say without risk of error that the septum was the final step, or one of the final steps, in the construction of a living chamber.

6. The first living chamber, or the first larval or næpionic 1 stage of a Nautiloid was, therefore, represented by the apex of the conch in that order; but the first septum and siphonal cæcum did not exist at this stage, which is represented by a straight or slightly curved widely spreading cone, — in fact, the empty apex of the conch. The length of the first living chamber has not been ascertained; but that it was short seems probable from the form of the cone in Nautilus. Doubtless this remark does not apply to the earliest forms of closely coiled shells, in which the cone was much slenderer than in existing Nautilus, and the first living

¹ Nήπιοs, infant, or young animal. The term "silphologic" was used for this stage in the article above quoted. This literally means "grub" stage, and it is not strictly applicable to a normal progressive stage of development. Grubs, caterpillars, and the like, among insects, are degraded or retrogressive developments, as compared with the normal, probably hereditary Thysanuriform larvæ of what are commonly called the lower orders of Insecta. Studies of insects lately made have convinced us of the truth of this opinion, first published by Friedrich Brauer, and of the need of changing this term to the one used, and of reserving silphologic as a general term for retrogressive stages, such as one finds in the larvæ of Coleoptera, Lepidotera, Hymenoptera, and Neuroptera.

chamber perhaps longer in proportion. The entire absence of a cœcum, and of all signs of a siphon, may be inferred with probable certainty in this first stage; and we proposed, in the paper referred to above, to name it the Asiphonula. This form may indicate the previous existence of a common univalve ancestor for the Cephalopoda which resembled the Pteropoda. Certainly the aspect of the calcareous protoconch of Ammonoids and Belemnoids favors this idea, first suggested by Von Jhering; and the asiphonula adds another argument, since it has no siphon or

Fig. 1-3. Apex and protoconch of Orth. elegans, Münst., from the side, below, and in front. In Fig. 2 the fine striae radius cross the shoulder of the apex (b), and reach to the protoconch (a). Named by Klipstein, Loc. St. Cassian, Coll. British Museum.

Fig. 4, 5. Apex and protoconch of another specimen mounted with the first on the same card. Named by same, Loc. same, Coll same

Coll. same.
Fig. 6-8. Views from the side, front, and below of the same parts in Orth. politum, Klipst. The shading on the protoconch of Fig. 8 does not indicate structure; this protuberance is smooth. a, protoconch; b, shoulder of the area of the cicatrix. Named by same, Loc. same, Coll. same.

true septum. The young of the Pteropoda, especially the ancient forms, had calcareous protoconchs in most forms; but doubtless there are more primitive shells in which the protoconchs had the more primitive, embryonic, conchiolinous stage of development. The evidence, therefore, is not conclusive, but it justifies the supposition that Cephalopods and Pteropods had originally some common ancestor, a true shell without septa or siphon, and possessing a protoconch, which might have been conchiolinous.

There is, however, another group, the Scaphopoda, which may claim to be considered in this connection. According to W. K. Brooks, the veliger is represented by the adult of Dentalium in several of its leading characteristics, and this must be regarded therefore as the most generalized type of the true Mollusca. It is quite possible that the asiphonula may have retained some of the characters of the veliger, and may have resembled Dentalium or

some common ancestor, and may have descended from this form without having passed through any pteropod-like ancestral modification. The peculiar resemblances of the young of some of the Goniatitinæ and the adults of Tentaculites among Pteropoda may be entirely due to homoplasy, and not to homogeny.

<sup>&</sup>lt;sup>1</sup> These terms were first used by Lankester (Jour. Micr. Sci., XVII., 1877, p. 436). They express phenomena with which naturalists have long been familiar, "homoplastic" meaning representation and independent origin of similar characters, and "homogenous" meaning genetic connection. See also previous use of terms Heterology and Homology for the same phenomena by Cope, in his masterly essay, "Origin of Genera," Proc. Acad. Sci. Phila., 1865, and "Origin of the Fittest," p. 95.

It is obvious that we cannot account for the nautilus-like ventral saddle of the earlier sutures of the Ammonoids, the calcareous shell of the protoconch, the coecal stage, the absence of the collar in the lower Goniatitinæ and in the young of the higher forms, the often central position of the siphon in the young, and many other characters, unless we admit a probable derivation of the Goniatitinæ from some straight microsiphonulate form of Nautiloid. It is, therefore, highly probable that the pteropod-like aspect of the young of some Goniatitine may be a purely homoplastic charac-

be a purely homoplastic character, and be meaningless so far as the genesis of the group is concerned.

7. The next or second of the næpionic stages was represented by a living chamber, which was completed by the building of the first septum with its attached eæcum, indicating the primitive beginnings of a siphon. This stage we styled the Cæcosiphonula, and we have considered the possession of a cæcum to be an indication of the former existence of an ancestor having a central series of cæcal pouches. These may have had functional communication in some forms by means of an endosiphon, as in means of an endosiphon, as in the Endoceratidæ, and in others, either belonging to this family or to a more primitive group, they may have been closed cæca.

8. The next næpionic stage was ended when the second septum was built in the modern

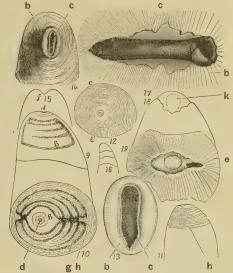
Endoceratidæ, and in others, situres.

Fig. 10. Apex of same species after the probably violent removal of the protoconch, showing the fractured shell (b), and the unusual aspect of the cicatrix. This and Fig. 16 are types. Loc. Yorkshire, Coll. British Museum.

Fig. 15. Apex of Coll. angus, Alma, near case.

Fig. 16. Apex of Coll. angus, Alma, near case.

Fig. 17. Apex of same species after the probably violent removal of the protoconch, showing the fractured shell (b), and the unusual aspect of the cicatrix. This and Fig. 16 are types. Loc. Yorkshire, Coll. British Museum.



Nautilus, and in the vast majority of all known fossils of the order so far known to the author this stage had similar characters. The siphon was larger at this stage than subsequently, and possessed a prolongation which reached down into and lined the primitive cocum. This closed pipe was however more or less cylindrical, and formed a transition to a cylindrical, open, siphonal tube, when compared with the cocum on the one hand and the siphon of the succeeding septa on the other. The second septum was prolonged apically into a funnel, and this was continuous with a true porous wall, which formed the remainder of the pouch. We have already pointed out the probability that this wall was the homologue of the calcareous sheaths or endocones which filled the interiors of the siphons of Endoceratidæ. There is, therefore, as previously stated by the author, a structural though highly concentrated and much modified remnant of the adult siphonal elements of an Endoceras still preserved in this stage, even in the existing Nautilus, and we propose to name it the Macrosiphonula.

9. The next napionic stage in living Nautilus was the third living chamber and third septum with its siphon. The siphon has a true funnel, and the siphonal wall attached to it is less swollen out, and seems, upon re-examination of the junctions at the opening of the funnel in the second septum, to be discontinuous. If we are correct, this stage has a small siphon consisting of the usual funnel and tubular porous wall, as in the vast majority of all Nautiloids and Ammonoids. We proposed to name this, according to its aspect and structure, the Microsiphonula. The microsiphonula, though a næpionic stage in the modern Nautilus, did not always occur among larval stages, but had in common with the macrosiphonula a traceable beginning in the adult stages of ancestral types. The genesis of the two forms of siphon may be studied in the Endoceratidæ. In this family Cyrtocerina had a siphon, which continually increased in size, probably throughout life, though more forms need to be described before one can be assured of this as a fact. There is no doubt, however, that the next form, Piloceras, had what we can safely call a macrosiphon of typical structure until very late in life. The large shells collected in Newfoundland by the author had siphons of great size, which were only slightly contracted or remotely approximated to the tubular condition of the Orthoceratide in the adolescent and adult stages.

This and other changes occurring in the adolescent stages induced us to distinguish them by a special term, Nealogic. The adolescent or nealogic stages, therefore, and the stages of the adult, or, as we have named them, the Ephebolic stages, in Piloceras show for the first time a tendency to contract the siphon or approximate to the microsiphonula, but they never had a true microsiphon. The contracted siphon in these forms, as in the other genera of this family, always had the holochoanoidal or complete funnel reaching from one septum to the next, and a series of conical concentric endocones, or sheaths, as they have been called by others, which stretched from the ends of the funnels, and were the homologues of the porous walls of the segments of the siphon in Nautilus.

The terminations of the endocones were prolonged into a central tube, or endosiphon, which we have previously described, and which probably served as a

functional siphon in these shells. Gerard Holm¹ first called attention to the interesting character of the young stages of the siphon in Endoceras, and has shown this organ to have been very large even in the young, having not only a cæcal beginning, as in other forms, but in several species having a swollen or macrosiphonulate form which endured throughout several septa. In specimens now in the Museum of Comparative Zoölogy, at least six septa were built before any signs of contraction began to appear. In other cases figured by Holm the siphonal cæcum, though very large as compared with that of Orthoceras, was attached to the first septum, as in all the shells so far known from that group, and occupied only the first air-chamber. We should suggest to those having materials for study, that the shells having this last character are very likely not true Endoceratites, but perhaps the young of species of the genus Sannionites, which, according to the classification followed by the author, is a genus distinct from Endoceras, because the species possess a much slenderer siphon. Whatever the fate of this suggestion, it is plain that transitional series exist in this group between Sannionites and Cyrtocerina or Piloceras, and that gradations occurred also in Piloceras, which show that contraction of the siphon began first in adults, and then, according to the law of acceleration, was inherited in the nealogic stages of immediate descendants, and finally became næpionic in the smaller siphoned species of the genera Endoceras and Sannionites. This tendency to contraction in the diameter of the siphon indicated the beginning of a series of transformations which accompanied a decrease in size of the fleshy siphon, and other correlative transformations, such as the decrease in length of the funnels, and the contraction and straightening out of the calcareous endocones, so as to form the walls of a tubular siphon. In other words, as the siphon contracted, the functional endosiphon formed by the open and extended tips of the endocones was finally brought into line with the funnels, and together with them formed the microsiphon, which is consequently a degraded modification derived from the funnels, endosiphon, and endocones of the Endoceratidæ. The Orthoceratidæ and all the remaining forms, with some notable exceptions which we shall take up and describe in future papers, had a microsiphon. The whole microsiphon formed a continuous open tube of narrow diameter, reaching from the last septum to the næpionic septa, which represented the macrosiphonula. Doubtless the duration of næpionic stages will be found to vary somewhat in ancient forms, but the indications, so far as known, are in favor of the theory that the vast majority of even ancient forms had a microsiphon, which was developed comparatively early in the life of the animal.

The nealogic stages of succeeding groups would be very interesting if there were space to describe them, but we shall have to illustrate this part of our work among the Ammonitinæ. The protoconchs of Ammonidea, including the genus Bactrites, had, as remarked above, globose forms with calcareous shells, and these shells were continuous with the apex of the conch, but the aspect of the junctions was quite distinct from those of Nautiloids. The constriction between them and the apex was very slight in the uncoiled young of the

<sup>&</sup>lt;sup>1</sup> Dames et Kayser, Paleontol. Abhandl., III., Part I.

more primitive forms of several silurian and devonian species of Goniatitinæ, and this is notably the case in Bactrites which has a straight shell. In these primitive forms the apertures of the protoconchs must have been less contracted than in most Nautiloids.

The apex of the conch did not expand so fast as in Nautiloids, but was more nearly of the same diameter as the neck of the protoconch, and often remained tubular for a considerable portion of the napionic period. This was especially evident in the more open whorls of the anarcestian larvae, figured by Sandberger, Barrande, and Branco. Among the close-coiled forms of paleozoic species, and in still later occurring genera, the protoconch itself became depressed, and a deep dorsal constriction resulted from the abruptness with which the apical part of the conch turned in upon the inner (dorsal) side of the protoconch.

The calcareous nature of the shell, the depressed form and transversely constricted aperture, and the closer union of protoconch and conch among Ammonoids, separated the young apparently so widely from those of Nautiloids, as to lead Barrande, Munier-Chalmas, and Branco to deny that transitions occurred between them. Another distinction of importance was, that the aperture of the protoconch was closed, not by an apical plate, but by the first septum. In other words, the asiphonula of Nautiloids disappeared as a distinct nepionic stage, and the excosiphonula took its place in the development of the young among Ammonoids. This fact led Branco in his masterly work on the early stages to assert, in common with Barrande and Munier-Chalmas, that the protoconch of the Ammonoids was the homologue of the apex of the conch and first air-chamber in the Nautiloids. Certainly the calcareous shell and the position of the first septum and execum appear to be in favor of their view.

On the other hand, the student of embryology will be slow to admit that the resemblances of the protoconch in Ammonoids to the veliger shell has no meaning. If it have any meaning at all, and can be compared with the protoconchs of the Cephalophora during the veliger stage, then during the whole of that stage the typembryos of Ammonoids, like all other veligers, could not have had a siphonal cacum or siphon. This is insured by the emptiness of the protoconch, the siphonal cacum being present only in the aperture, and not penetrating far back into or resting upon the first formed plate of the protoconch, as in the first air-chamber of Nautiloids.

Another argument in favor of the view here advocated is the general fact, cited in the paper quoted above, upon the "Values in Classification of the Stages of Growth and Decline," that the typembryos, to which class of forms the veliger belongs, cannot be said to have the essential characters of any specialized division, like the Cephalopoda, but have to be compared with remote and generalized types from whom their principal characteristics were inherited.

The authors quoted above, holding the view that the protoconch was the homologue of the first chamber and apex of Nautiloids, necessarily rejected our theoretical explanation of the presence of the first septum and cæcum in the aperture as due to acceleration of development.

Nevertheless, this explanation still seems to us correct, and we have now a new

point to make in its favor. If the protoconch of Nautiloids was an empty conchiolin shell and represented the veliger stage, it most certainly could not have been the ancestral form from which the calcareous tendency of the same stage in Ammonoids was derived. The characteristics of the asiphonula of Nautiloids are, however, just what are needed to fill the gap. The apex at this stage in Nautiloids is rounded and calcareous. The tendency to deposit calcareous matter could therefore have been inherited from an ancestor corresponding to the asiphonula, and which we will name the Asiphonophora. The Asiphonophora must have had a calcareous shell acquired as an adaptive character, without internal calcareous septa or a siphon. This form could not have been by any means so far removed from the ancestor of the veliger as the immediately following ancestor of the macrosiphonula, which we have named the Macrosiphonophora. This must have had septa and a central axis of cæca, or at any rate at least one septum and a cæcum.

The characters of the Asiphonophora, when transmitted to the Ammonoids according to the law of acceleration, would have been inherited earlier than in Nautiloids, would therefore have affected the growth of the protoconch, and would have necessarily produced the calcified shell of this stage in Ammonoids. The fusion of the protoconch with the conch in all Ammonoids was the immediate result of this process, and in this way the more tubular form and freer connection of the protoconch with the true conch, and the constant adhesion of the former to the latter, can be explained.

The disappearance of the asiphonula as a distinct stage in the young of the Ammonoids appears to us, therefore, not an argument against the derivation of the Ammonoids from Asiphonophora, but in favor of this opinion. In fact, it seems to us that, in order to disprove it, opponents will have to find a cicatrix upon the apex of the protoconch in the Ammonoidea. According to the uncompromising attitude of those who insist upon the naked facts, and are hostile to explanations, the protoconch is the apex of the conch in Ammonoids, and the absence of any cicatrix upon the tip of this is a difficulty they can only surmount by asserting that the general and special homologies we have traced, and all the embryological and næpiological correlations, are purely homoplastic, and do not indicate the derivation of the Ammonoids from any form of Nautiloid. They must also explain away the similarity of the protoconch in external aspect to the veliger shell in Gasteropoda, since this is an earlier stage than that of the apex of the true conch in Nautiloids, Ammonoids, and all cephalous mollusks. Can any of these gentlemen tell us why the cicatrix does not appear upon the protoconch of Ammonoids, and explain at the same time how that shell came to be similar to the veliger shell in the Cephalophorous Mollusca on the one hand, and the apex of the conch of Nautilus on the other?

It must be observed, also, that we do not insist that the primary radical of the Ammonoids, Anarcestes, was necessarily descended directly from Endoceras, but that it had probably come from a prototype like the veliger, possibly, as suggested by Brooks, from a class now only represented by the genus Dentalium. The next step, according to our translation of the evidences, must have been the Asiphonophora, which may have been more of a Pteropod or Scaphopod than a Cephalopod. So far as the shell goes, there are no similarities to the peculiar shell of Dentalium, but perhaps more to that of a Pteropod.

The next step in this line of genesis must have been the ancestral generator of the characters of the caecosiphonula, which we propose to call the Caecophora, a form which must have been a reality in some shape, and in some species doubtless had the characters of the caecosiphonula in its ephebolic stages. This class of forms, though having septa and a central axis, which we might have to consider as a primitive siphon, was nevertheless quite distinct from those which followed.

The next link in the genealogical tree must have been the ancestor of the peculiarities of the macrosiphonula, and this is luckily a well known form. The Endoceratidæ enable us not only to see that the previous train of induction is legitimate, but to connect our line of hypothetical forms with the next in the evolution of the group. The Endoceratidæ are true Macrosiphonophora, according to the nomenclature adopted here, and are transitional to the more highly specialized and stable modification which had what we have termed the microsiphon.

When this organ came into being in the direct line of change, the evolution of the forms also changed its character. The more rapid or accelerated modes of change were replaced by slower processes. The changes occurring in the types preceding, and including the Endoceratidæ (Macrosiphonophora), were, if we can judge by the abrupt transitions of the genera in this family, more rapid and more important in their effects on structures than was the rule subsequently. This is also shown in the structural changes taking place in the embryos of Nautiloids and Ammonoids, as compared with the slow and comparatively slight changes of the subsequent stages of growth. The rapid acceleration of the macrosiphonulate character during the evolution of the Endoceratidæ, the still more rapid acceleration which took place in the evolution of the microsiphon among Ammonoids, and the fusion, through acceleration in development, of the characters of the asiphonula with the protoconch, all bear witness to the truth of this induction.

The næpionic stages in ancient asellate forms of the Ammonitinæ, as has been shown above, may be considered as indicating the primitive radical, the straight orthoceran, and the gyroceran, or loosely coiled nautilian shells; but in

We have already traced the more rapid evolution of the ancient forms of Cephalopoda, and need not go into the matter any further in this monograph than to state that these facts accord with the law announced in Genera of Fossil Cephalopods (Proc. Bost. Soc. Nat. Hist., XXII. p. 262), which reads as follows: "These facts, and the acknowledged sudden appearance of all the distinct types of Invertebrata in the Paleozoic, and of the greater number of all existing and fossil types before the expiration of paleozoic time, speak strongly for the quicker evolution of forms in the Paleozoic, and indicate a general law of evolution. This, we think, can be formulated as follows: types are evolved more quickly, and exhibit greater structural differences between genetic groups of the same stock, while still near their point of origin than they do subsequently. The variations or differences may take place quickly in the fundamental structural characteristics, and even embryos may become different when in the earliest period, but subsequently only more superficial structures become subject to great variations." See also Foss. Ceph. Mus. Comp., in Proc. Am. Assoc. Adv. Sci., XXXII., 1883, p. 338.

all other forms, especially in the devonian latisellate and triassic angustisellate embryos, the tendency to become closely coiled, and to inherit the depressed primary radical whorl of Anarcestes, produced the Goniatitinula, and affected even the protoconch. The protoconch through heredity becomes depressed fusiform by lateral expansion in the Angustisellati, and the embryonic nautiloid character of the first septum in the asellate forms and its tendency to form a broad ventral saddle in the latisellate and a narrow ventral saddle in the angustisellate embryo is correlative with this progression of form.

The goniatitinula is a true larva, corresponding to adults within the order. We use the term because it is the characteristic larval form of the Ammonoidea, which was introduced at first among adult Goniatitine, and in the higher forms of this group became, by acceleration, fused with the microsiphonula.

The remarkable researches of Branco enable us to state that this progression in complication of the embryo in form and sutures has no counterpart in the parallel series of any pre-existing series of adult shells, except among Nautiloidea; consequently the angustisellate peculiarities of the ventral saddles and deep lateral lobes characteristic of the latisellate and angustisellate embryos of the Devonian and Trias were not due to inheritance from primitive adult radicals, but were later modifications originating in the cæcosiphonula from close coiling. They were correlative with the earlier or accelerated development of the depressed whorl, and the quicker growth in bulk of the whorl. Similar tendencies have been observed repeatedly in different progressive series of Nautiloidea. Thus, wherever we have been able to trace the series of species from a straight, or loose-coiled, to a close-coiled nautilian form, this as a rule has more complicated sutures. The universal result of such progressive specialization among the adult forms of Nautiloids is closer coiling, due to quicker growth in bulk of the whorl, and is accompanied also by the evolution of a larger ventral saddle. It is not surprising that similar mechanical results should follow in the septa of the embryos of Ammonoidea, when similar changes in the mode of growth occurred through the accelerated inheritance of the depressed anarcestian radical whorl, and closer coiling in the cæcosiphonula.

Branco has observed the shortening of the larval stages in the Latisellati as compared with the Asellati, and the still greater acceleration of development occurring in the Angustisellati, and the correlation of these with the general progress in complication of the sutures of the adults of the same divisions in time. This confirms our previously published opinions of the relation of embryos and adults, and also agrees with those here published regarding the inheritance of the primary, radical, smooth form in the depressed embryos of Latisellati and Angustisellati, and the correlative evolution of the sutures and coiling.

The microsiphonula appeared in the Ammonoidea with the second septum, in what is morphologically the second air-chamber when compared with Nautilus, though actually the first existing in the apex of the true conch. This microsiphonula is also an accelerated form, since the siphon becomes very rapidly or even abruptly attenuated. The collar or distinctive organ of the siphon among the normal Ammonoids was not formed until later, though the precise period

has not been ascertained in any one form, so far as we know. The microsiphonula occurred, as might have been expected, earlier than the true goniatitic stages, or goniatitinula, in those species which had the nautiloidean stage with ventral saddle also prolonged into the second septum, as in the Asellati figured by Sandberger, and *Gon. atratus* figured by Branco. The goniatitinula became distinguishable when the first ventral lobe appeared. This was undivided, as in the lower Anarcestes and in the Magnosellaridæ among Goniatitinæ. This stage is prolonged through one or more septa in the higher Goniatitinæ, and also in the Lytoceratinæ and Ammonitinæ, and the whorl also at this time strikes one as similar to Anarcestes, or depressed semilunar in section, as stated above, and in these the goniatitinula is completed.

The duration of the næpionic period can in a general way be described as coincident in extent with the duration of the smooth shell, which is always found at the centre of the umbilicus, however much the shell may be subsequently ribbed and ornamented. This period would of course include many more transformations than the goniatitinula, especially among the higher and later occurring species of the Mesozoic.

Haeckel designated all of the progressive stages which succeeded the true ovarian stages and included the næpionic and nealogic stages, and their structural relations, under the term Metamorphology.1 This term is, however, somewhat indefinite and artificial when limited in this way, since the ovarian stages are necessarily of very different duration in distinct groups, and cannot be considered as the natural limit of the embryologic period. We should, as above stated, be disposed to think that some such limit as here proposed would be nearer to the true one, namely, to consider the typembryos as the last of the true embryologic stages. This nomenclature would enable an author to give an approximate idea of the stage at which the metamorphologic stages began in any type. Thus, they would have begun in Nautiloids with the asiphonula, and in the absence of this among Ammonoids with the cæcosiphonula. In the absence of this last, if it is absent among the lower Sepioidea, the metamorphologic stages, according to the same rule, would begin with the first stage immediately succeeding the protoconchial stage. Whenever this last is absent, as it certainly is among the highest of the Sepioidea having meroblastic ova, then its equivalent stage, which represents what is left of the veliger, should be taken as the last of the embryologic stages.

As has been noted above, the næpionic period is always smooth, and is visible at the centre of the umbilicus in most discoidal shells, and the demarcation is therefore visible between this and the nealogic period; but, as can be observed on most specimens, an attempt to separate the characters of the latter from the characters of adults is attended by greater difficulties. It is, however, essential to distinguish the category of ephebolic or adult characters from the nealogic, because in each form of any series there are usually found certain novel characters, which appear for the first time in that particular series. These make their first appearance almost invariably during the ephebolic period.

<sup>&</sup>lt;sup>1</sup> Morph, d. Organismen, II. p. 22.

The ephebolic characters are as a rule inherited or homogenous within the special series in which they originated, but are not transmitted from one series to another except through the medium of the nealogic stages of what we have called the *tertiary radicals*, and they are not, so far as we know, ever concentrated in the earliest larval or næpionic stages; they occur too late in the history of types.

We classify in the nealogic and ephebolic stages such characters as follows: the sharply defined ridge-like pilæ and tubercles, the channels with their lateral ridges, and keels, and especially the hollow keel, the highly developed rostrum of the higher suborders, especially Ammonitinæ, the lateral lappets of the apertures, and the branching marginal lobes and saddles of the sutures of suborders above Goniatitinæ. Speaking in a general way, we should include in these categories those progressive characters which appear late in the life of the shell among the higher suborders, and at the acme of their development in time, which are not found in the stock of discoidal radical forms. When the shell began to assume the ribs or pilæ, as we prefer to call them, the nealogic period may be said in a general way to have been entered upon. It has been found that these stages of growth indicated genetic relationship with radical forms, which were not infrequently merely different genera or species within the limits of the same family, and often occurred on the same or only slightly different horizons. The nealogic stages of the higher Ammonoids, Ammonitinæ and Lytoceratinæ, have not the constancy and general importance of the næpionic stages, but are transient in the history of the types, appearing and disappearing in the same limited series of forms. They consist of the less important modifications which first appeared in the adolescent or adult stages at a late period in the history of a type, and were then inherited in the nealogic stages at earlier ages in successive species of the same series, according to the usual action of the law of acceleration. The nealogic category cannot be as definitively separated from the characteristics of adults as from those of the larvæ. Their first appearance in adults indicated the establishment of a new species in any given series, since they are invariably differences so far as their predecessors and congeners in the same series are concerned. However much they may represent or reproduce the characters of species in other series, they are essentially differentials as regards the adult stages of ancestral species of the same series. Thus the nealogic characters are as a rule ephebolic, and not nealogic, in origin among the Cephalopoda, and usually become nealogic through inheritance. We shall have frequent occasion farther on to call in the evidence of the ephebolic stages, and to show, as in the Endoceratidæ, that, as a rule, characteristics originated in this stage of growth, as indeed must have been the case with the cæcum and the microsiphon.

At the termination of the progressive stages, which ended with the full development of the ephebolic characters, the first stage of decline, or the geratologic period, began to make its appearance, and became more and more apparent as the specimens advanced in age. It was found that, as has been observed

<sup>&</sup>lt;sup>1</sup> See, for secondary and tertiary radicals, p. 22 et seq.

in other animals, especially in man himself, the decline was marked by degradation of certain characters, and the number of parts undergoing degeneration was gradually increased, until finally the whole of the body was more or less affected.

This period has been frequently described by the author in previous publications, and will be more fully described farther on. It is necessary now only to call attention to the fact, that the geratologic or old-age period can be naturally subdivided into two quite distinct stages. The first, or Clinologic stage, included the retrogressive transformations during which the nealogic and ephebolic characters became resorbed one after another, usually in reverse order to the succession in which they were introduced during the progressive stages of growth. The size of the whorl also, sooner or later according to the species, showed retrogression during this period. All of these retrogressive tendencies reached their extreme expression in the last and final stage of the ontogeny of the individual. In this stage the spines, pile, and often the keel and channels, when present, were lost, and the size of the whorl was so much reduced in all its diameters that it became more or less rounded, whatever the angularity of the whorl during the ephebolic period. This stage we have designated by the term Nostologic, on account of the likeness to its own næpionic period, which was finally acquired by the smooth, almost rounded whorl after the loss of its progressive characters.

Geratology, or the study of the relations of these old-age stages, shows, as we shall try to demonstrate farther on, that the clinologic characters can be used to predict the degradational modifications which appeared in any series of ornamented shells when placed under such unfavorable conditions that their descendants became degraded, and series of more and more retrogressive forms were gradually brought into existence. A number of such series have been traced by several authors, and they usually end with a perfectly straight form. This form terminated the phylogeny of the series in a manner comparable to that in which the nostologic stage terminated the ontogeny of the individual. It is usually separated also by a gap from all other species, which has not yet been fully filled by intermediate species. This nostologic adult form, the so-called genus Baculites, is not only comparable in this way and by means of its smooth and compressed cylindrical whorl with the last stage of ontogeny, but it is also a very complete reversion to the aspect of the earliest radicals of its own class, the Orthoceratite and Endoceratite.

This nomenclature is similar to that originated and published by Haeckel, and at first sight may appear to many naturalists as identical; but it is really only complementary. It is based upon strictly structural and morphological grounds, whereas Haeckel's nomenclature¹ was entirely physiological. This eminent author regarded the ontogeny of an individual as a cycle divisible into three periods; first, the progressive stages of Anaplasis, or those of progressive evolution; secondly, the stages of fulfilled growth and development, Metaplasis; thirdly, those of decline, Cataplasis. He also appreciated and gave full weight to the general physiological correlations which are traceable between the history of a group and

<sup>&</sup>lt;sup>1</sup> Morphol. d. Organismen, II. pp. 18-23.

the life of an individual, and in accordance with these ideas designated the progressive periods of expansion in the phylogenetic history of a group as the Epacme, the period of greatest expansion in number and variety of species and forms as the Acme, and the periods of decline in numbers of species, etc., as the Paracme.

Haeckel used also the term Anaplastology for the physiological relations of the stages of progressive growth and those of the epacme of groups, Metaplastology for those of the adult and the acme of groups, and Cataplastology for those of the senile stages and the paracme of groups. These terms seem to cover the same ground as those we have employed, but they were in reality chosen for the purpose of classifying physiological relations. Thus the anaplastic relations of the næpionic and nealogic stages to the phenomena occurring during the epacme of groups, the metaplastic relations of the ephebolic stages to the phenomena occurring at the acme of groups, and the cataplastic relations of the geratologic stages to the phenomena occurring during the paracme of groups, are the functional relations of the structural modifications occurring in the ontogeny of individuals to those which are characteristic of the phylogeny of groups.

# THEORY OF RADICALS AND MORPHOLOGICAL EQUIVALENCE IN PROGRESSIVE FORMS.

The simpler characters of the sutures in the adults of more ancient forms, as compared with the more modern species of the same series, has been noticed by Würtenberger, Zittel, Neumayr, Waagen, and Branco, in different groups of Ammonitinæ. The first is very decided in his statement, that the Ammonitinæ he has studied form perpetually diverging series, which spring from certain common ancestral forms.

The constant repetition of discoidal and involute forms in series, which are otherwise distinct in respect to their sutures and minor characteristics of development and shell markings, produces a similarity in the succession of the forms. It is practicable to compare the evolution of discoidal into more involute forms of any one series with a similar genetic procession in any other series. Thus in the General Summary, Plate XIV., we can compare the discoidal forms of Ver. Conybeari, Fig. 20, with Arn. tardicrescens, Fig. 26, Cor. rotiforme, Fig. 30, and Ast. Turneri, Fig. 36, and in the same way the involute forms of Ast. Collenoti with Oxyn. oxynotum, Greenoughii, and Lotharingum; and these comparisons also hold good for Schlot. Boucaulliana, and the terminal forms like Wæh. Emmerici and Psil. mesogenos, which are also involute. In exceptional series the whorls do not become more involute in the higher species, but are nevertheless modified in those characteristics which usually accompany and correlate with increase of involution. Thus the lateral diameter of the whorl decreases, the sides become more and more

<sup>&</sup>lt;sup>1</sup> Würtenberger, Stammesgesch. d. Amm., Darwinistische Schriften, Nr. 5, Leipzig, 1880, p. 91. Zittel, Ueber Phylloceras tatricum, Jahrb. d. k. k. geol. Reichsant., 1869, p. 65. Neumayr, Die Phylloceraten d. Dogger und Malm, Ibid., 1871, pp. 347, 348; also, Zeits. d. deutsch. geol. Gesellsch., 1875, p. 866. Waagen, Permenreihe d. Amm. subradiatus, Benecke's Geognost. paleont. Beitr., II. p. 202. Branco, Paleontogr., XXVI., XXVII.

convergent outwardly, and the abdomen narrower, though the shell may still remain discoidal; ex. Caloceras and Coroniceras, Plate XIV. Fig. 11-16, 28-32.

The Ammonoids of the Lias also have a tendency to produce keels, ribs, etc. in addition to the parallel procession of the forms just described. Thus, when we study the parallelisms occurring in different series or genera of the Ammonitinæ in the same family or group, we find that equivalent species in different series are due not only to the increasing involution of the whorls, but also to the development of similar structural characteristics. Most palæontologists are not aware of these facts, and therefore are apt to consider species of distinct series as closely allied. It is usual, for example, to classify all the species of the Arietidæ having quadragonal whorls, deep channels, prominent keels, and well developed pilæ, as species of the same genus, Arietites, whereas they are more closely allied to Psil. planorbe, their radical ancestor, than they are to each other. Errors of this kind are common, and have been still more general. Thus most modern improvements in taxonomy in all the branches of the animal kingdom have consisted in doing away with classifications made by the association of representative forms, or, as they are here called, morphological equivalents.

The Arietidæ sprang from discoidal species of Psiloceras, having smooth shells and phylliform sutures. Other groups occurring later in time are traceable to forms of more advanced structure, so far as the shape and ornaments of the whorl and the sutures are concerned. In every case, however, progressive groups have been traced directly to forms having discoidal shells. The discoidal radicals of different series have been invariably found to be nearly related to each other, and to preceding discoidal radical types, while their descendent species are divergent, and essentially distinct. However closely they might have resembled each other as morphological equivalents, they possessed the homogenous differential characteristics of their own genetic series.

I have elsewhere noted the facts tending to establish the probable existence of a continuous line or radical stock of types or species.<sup>2</sup> The paleozoic primary radicals are similar to Anarcestes; the mesozoic or secondary radicals are like *Dinariles Mahomedanus*, *Ceratiles Sturi*, Gymnites, and Psiloceras; they occur largely in the Trias, and are species with discoidal but rather compressed smooth shells. The tertiary radicals, though discoidal, may be highly ornamented with pilæ and spines, and have sometimes very broad or coronate whorls; they occur largely in the Jura.<sup>3</sup> The primary and secondary radicals, if we follow Haeckel's nomen-

<sup>1</sup> Zittel's Handbuch d. Pal., I. p. 455.

<sup>2</sup> Gen. of Foss. Ceph., Proc. Bost. Soc. Nat. Hist., XXIII., 1883, pp 323-325.

<sup>\*\*</sup> Tirolites and Tropites are aemic or tertiary radicals occurring in the Trias. They are certainly coronate forms, with pilæ, tubercles, and open umbilici. If any one will compare the young of Balatonites or Tropites with the adults of the smooth species of Dinarites and Ceratites as figured by Mojsisovics, he will be able to see that the radical stock is a definable series of forms, with characteristics not only shown in the adults of simpler smooth genera and species, but necessarily repeated in the young of more modified species, like Balatonites, Tropites, etc. It must be remembered, however, that all forms will not have the smooth, compressed secondary radical reproduced in their young; many of them lost this, or had it only very slightly, since it was replaced by the broader-abdomened tuberculated tertiary radical, as in the young of Trachyceras aon. The young of Tropites has a form and sutures similar to those of Glyphioceras diadema of the Carboniferous, and the stock of tertiary radicals may therefore be said to have begun even in the Paleozoic.

clature, are epacmic, and the tertiary are what we should call acmic radicals. Cwl. Pettos is an excellent example of an acmic radical in the Jura. It stands morphologically and chronologically at the centre of the affinities of the group of Dactyloidæ and Stephanoceratidæ, that is, of the larger part of the oölitic Ammonitinæ. It is, in its relation to these, and to the characteristics of their nealogic stages of development, an epacmic radical, but with regard to Psiloceras, and more ancient secondary radical forms, it is a tertiary or acmic radical. It has a flattened abdomen, very divergent sides, like those of Steph. coronatum, and similar acmic radical forms, and a line of coarse tubercles along the sides. Though altogether distinct from Psiloceras, it is also a perfectly discoidal form. The direct descendants of Pettos, which belong properly to the stephanoceran and allied groups, are also discoidal forms, though the series often have involute species, such as Macr. macrocephalum, etc.

Tertiary radicals in what we propose to call the Pettos Stock, or Spinifera, according to the evidence of the younger stages and the characteristics of adults, have but one row of large spines in adults, and whorls which are very gibbous or trapezoidal in section, that is, with abdomen broader than dorsum. The whorl may sometimes be smooth, with only one row of lateral spines, but is usually strongly pilated, the pilæ being single on the sides and as a rule bifurcated only on or near to the abdomen. The sutures have a more or less close resemblance to those of Der. Dudressieri, or Cal. Pettos. The line of descent being broken, we shall, in the imperfect list below, give some forms having two lines of tubercles. These, however, have young which, until a late stage, show only one outer line of lateral tubercles, as in the adults of the two species cited above. Steph. nodosum of the Lower Oölite is the tertiary radical of that genus, and of Macrocephalites, Sphæroceras, Morphoceras, Reineckia, Cadoceras, Quenstedioceras, Aspidoceras, Olcostephanus, and Pachydiscus. All of these genera have some forms which are either closely similar to the radical in the adult stages, or else have young with a nodosum-like stage. Peltoceras athleta has a similar history, though it is like Dactylioceras in its nealogic stages, it has two lateral rows of large spines, and is similar to Asp. perarmatum in the adult. The huge coronate forms of the Upper Jura, like Olcostephanus Gravesianus, etc., and the singlespined forms like Aspidoceras Edwardsianus, and shells like Asp. perarmatum, Rupellense, etc., with two rows of spines, are obviously in the line of stock forms. In fact, one can select from the discoidal shells of these groups a more or lessclosely allied series of stock forms, from each of which a separate genus or series of genera arose, until we find in the Cretaceous a new beginning in Hopkites Royerianus and Cornuelianus for the species of that large genus, and of Acanthoceras, Pulchellia, and possibly Holcodiscus and Costidiscus.

The cretaceous group, with nodose keels or lines of tubercles in place of a keel, also belong to the Spinifera, but they form a separate phylum connected, in common with such forms as Acanthoceras mannillare, with the Hoplites series, and their radical is also Royerianus. The radical of Cosmoceras, Cos. Taylori of the Lias, is a species with two rows of spines allied to Deroceras armatum, and the adult characteristics of this species are repeated in the young stages of the

normal forms of that genus. Würtenberger has come to similar conclusions, and has traced a large part of the same genera back to the same origin in the work quoted above. We differ in details, and in the way in which we treat the stem of stock forms, but these differences will probably disappear after further researches have been made. His book is full of the evidences of careful work, and we do not feel disposed to offer any criticisms until there is an opportunity to publish our own observations in detail. The young forms of the Spinifera in the later næpionic stage, have a very close resemblance to the young of Tropites before the keel appears, and also an obvious reference to Tirolites of the Trias, and to the more remote and possible ancestor, Glyph. diadema, in the Carboniferous.

Per. Defranci is the radical of all of the species of the large genus Perisphinctes, and has no tubercles in the adult, but in the young there is a prolonged stage like the adult of discoidal coeloceran species, and in still younger stages a pettos-like stage. This genus embraces a very large number of species which have been traced out by Würtenberger, and referred by him to a species closely allied to the one quoted above in the Lower Oölite. The absence of tubercles, and the rounded form of the whorl in this group, and the frequent absence of the trapezoidal form and tubercles even in the early stages of many species, show that it is distinct from the Spinifera. We propose to designate it by the term Plicatifera.

The tertiary radicals of the keeled groups, the Carinifera, as we propose to call them, have also close structural relations, but are modifications of what we have called the quadragonal form. Nevertheless, in the young and the adults there is a tendency to reproduce the tertiary radical of the Spinifera. This is to be seen in Wähner's figures of Caloceras (Arietites) Coregonense, and that keen observer describes the resemblance of the young just before the keel appears to Cwl. Pettos of the Middle Lias. Similar facts can be noted in the young of other forms of the Arietidæ, but the keeled stage acquires prepotency in the Arietidæ. Their quadragonal, keeled, and channelled forms began in Caloceras, and from this genus sprang the similar tertiary radicals of the later Jura. The radical stock is continued by such species, as follows: Amaltheus Huwskerense, Phymatoceras enervatum, Hildoceras Walcoti, and Harpoceras Sowerbyi, which last has a modified quadragonal form until a late stage of growth in some varieties. Oppelia hecticus also has in some varieties a quadragonal form until a late stage, though not so discoidal as most of the preceding. In the Cretaceous, there is Schlænbachia tricarinatus and Westphalicus, which are true stock forms of the Cariniferæ.2

Haploceras, Desmoceras, Silesites, Pictetia, and the like, have tertiary radicals similar to the typical forms of Lytoceras, and belong therefore to the Lytoceratinæ.

<sup>&</sup>lt;sup>1</sup> Mojsis, et Neum., Beitr., VI., 1888, pl. xxii.

It should be noticed in this connection that the characteristics of the so-called pettos-like young of the earlier occurring species of the Carinifera are favorable to Mojsisovics's view that the Arietidæ sprang from Halorites. This genus is closely related to Tropites, and the form and sutures of the young of several species in the Arietidæ certainly show affinities for Tropites. On the other hand, as we have maintained above, the affinities and gradations of all the species of the Arietidæ lead us back into Psiloceras, and the alliance of that genus with Gymnites seems to be closer than with any other in the Trias.

Cal. tortile, Cal. luqueum, and Schlot. calenata, in the Plicatus Stock of the Arietidæ, are more closely allied to one another and to Psil. planorbe than are the morphological equivalents among their descendants to one another. However closely the descendent involute forms may simulate one another, their næpionic and nealogic stages are generally distinct, and indicate the series with its peculiar differential characters. Arn. miserabile or semicostatum, and Agas. lavigatum, are more nearly related to each other and to Psil. planorbe in the Lævis Stock than are any of the descendent morphological equivalents. There are several forms closely representative of one another, and apparently almost identical, among these morphological equivalents. Thus the adults of Ver. Conybeari are apparently very closely allied to Cor. bisulcatum, and to some forms of Ast. Turneri and Arn. ceras; but all of these are more distinct in their nealogic stages than in the adults. The Arietidæ present in this respect a similar picture (Summary Plates) to that of the whole group of the fossil Cephalods. Thus the adults of the earlier and simpler radical species, from which the later and more complicated forms must have been derived, are more closely related in structure than any of their adult descendants. The Cyrtoceratites, Orthoceratites, Gyroceratites, the Nautilini, and the anarcestian Goniatites of the Silurian, are more nearly related in structure and development, in the similarity of the adult sutures, the absence of pilæ and tubercles, and the mode of growth, than are their direct descendants, the genera of the Nautiloidea and the Ammonoidea in the Carboniferous and Jura.

The Nautiloids and the Ammonoids had morphological equivalents, but close parallelism is not constant or frequent, and occurred principally among later forms. We have elsewhere discussed this question, and need only notice well known cases; such as the extraordinary likeness of Clydonautilus to the higher forms of Goniatitinæ due to its divided ventral lobe, of Centroceras to Agoniatites, and of Subclymenia to Agoniatites, and also the better known example of the Clymeninæ of the Devonian and the Aturia group of the Tertiary. Such cases of morphological equivalence are disposed of by the use of the convenient expression, that these are mere analogies. This expression, however, fills nothing but a verbal gap. It neither explains parallelisms, nor the confusion they have occasioned and still occasion in our classifications, nor the constant tendency of straight shells to become coiled and of already coiled discoidal shells in progressive series to become involute, to whatever series they may belong, or wherever they may be found, thus producing morphological equivalents in great numbers.

The only comparison that represents all these relations to my mind is that of a number of divergent branches united at their bases or radical ends into a common trunk. The branches are composed of groups, which, though distinct, and having differential characteristics, are nevertheless similar in the forms produced, and in the order of procession of these forms.

The equivalent forms of the larger branches would be admitted to have originated independently of the direct influence of inheritance. We think that this is also true in the smaller series, since in no case can the similarities of the

equivalents, however close, have been derived or carried across the genetic lines of descent from an equivalent representative species of one branch to that of another. Nor could the similarities of such forms have been derived in any series from the radical species, because involved whorls, keels, channels, etc. did not exist in the discoidal stock forms. Parallel series and equivalent forms, also, occur often in such zoological and geological relations that any sequence or descent of one from the other is improbable; as, for example, Aturia of the Tertiary, and Clymeninæ of the Devonian; or Centroceras of the Devonian, or Subclymenia of the Carboniferous, and Agoniatites which began in the Silurian.

These facts speak with great force for the continuity in descent of the discoidal shells, and for the existence of a primitive trunk line of generalized radicals, beginning with the earliest times and lasting into the Jura. The universality of the phenomena leads at first to the supposition that we can account for morphological equivalence of species in different series by some invariable law of growth, such as is evidently the cause of the more exact parallelisms which occur between different individuals of the same species. We might consider each species as representing a hereditary grade of structure in the development of a series, just as any period in the life of an individual would represent a stage of development inherited from some ancestral form.

We were led into this error at first, but it is an inadmissible supposition in the light of the facts given above. These show, that the representative forms are absolutely new forms in their respective genera or groups, possessing characters not found in the stock or chronological trunk of discoidal radicals, and their resemblances are therefore homoplastic, and not homogenous.

There are also many kinds of series among fossil Cephalopoda, and in some of these forms similar to those of the Ammonoids and Nautiloids are not produced, as in the Sepioids and Belemnoids. In these orders entirely new modifications accompanied equally complete changes in habits and habitat. The crawling and shell-covered, littoral, radical Orthoceras has in these orders become changed into a swimming and predatory mollusk, the shell having become internal. It seems evident in these cases, that the forces of the surroundings and new habits deflected the Sepioids and Belemnoids from the more normal course taken by the Nautiloids and Ammonoids, and thus made the repetition of form or equivalence in the shells impossible, except very rarely, and then only in a very limited sense. Such, for example, are the similarities which exist between the internal shell of Spirula and the external shell of Lituites, or between the pseudo shell of the female Argonauta, and the true external shell of one of the compressed Ammonitinæ, like Cosmoceras or Hoplites.

The disappearance of the siphon in the Sepioids, and the naked young of the existing forms of this order, show that too much weight can hardly be given to the modifying and eventually controlling influence of changes of habit, or, what is the same thing, the effects of the surroundings in any new habitat, whether

<sup>&</sup>lt;sup>1</sup> See Evolution of Cephalopoda, Science, III., No. 52, 53, 1884; Foss. Ceph. of Mus. Comp. Zoöl., Bulletin, I., No. 1; Proc. Am. Ass. Adv. Sci., XXIII., 1883, p. 341.

sought by the animal or forced upon it by geologic changes. Professor Cope,1 in his masterly work on the "Origin of the Fittest," and in pamphlets previously published, described "homologous" and "heterologous" series equivalent to what we have called homoplastic and homogenous series, and gives numerous instances from all departments of the animal kingdom of exact and inexact parallelisms sustaining the position taken above. This eminent author discusses at length the location of growth force due to use or habits, and shows this to be an efficient cause of modification, thus bringing out clearly and demonstrating a new law of variation. His opinions with regard to "mimetic analogy" in external and internal characters differs only in so far as we have preferred to use the term morphological equivalence, because we thought it expressed more exactly the phenomena of homoplasy. He says (p. 96), "I believe such coincidences express merely the developmental type common to many heterologous (homoplastic) series of a given zoölogical region." With regard to the effects of habit, we should also refer to Cope's remarks (p. 198), and examples with which he explains the origin of generic characters in the ossification of the cranial walls in the Batrachia, and the origin of horns among Ruminants, as due to habits of defence, concluding (p. 200) that the use of the angles of the parts in question (the head) would result in a normal exostosis of a simple kind in the frogs, or as horn cores in the Ruminantia. Waagen, in his "Jurassic Cephalopoda of Kutch," 2 has made a valuable contribution to the facts in tracing several parallel series of Lytoceratine in India and Central Europe. "The most important facts which result from the investigations explained in the present volume are these two: first, that in Kachh, in the same manner as in Europe, developmental series exist, which are in part identical with the European ones; and second, that the succession of the identical species in time during the jurassic period in Kachh has been governed by exactly the same laws as have been observed in Europe."

"For facts (parallel series 3) like those mentioned, which would be augmented by a good many instances if other groups of Ammonites were as well known as Phylloceras, the only explanation is, that the changes of form in the organic world were dependent upon laws which were innate in them and had not to rely exclusively on outer circumstances. The latter factors, as struggle for existence, geographical separation, etc., certainly influenced the production of forms greatly; but the fundamental law upon which these influences acted very likely was not the law of variation, as stated by Darwin, but the law of development, or the tendency of the organisms to produce an offspring varying in a certain well defined direction. If this law be true, the time will come when we shall be able to indicate a priori, with tolerable certainty, what species a given form can or might produce."

Origin of Genera, Proc. Acad. Nat. Science, 1863; Methods of Creation, Ibid., 1871, p. 229; and Origin of the Fittest, p. 95 et seq.

<sup>&</sup>lt;sup>2</sup> Paleontol. Ind., Juras. Fau. of Kutch, I., Ceph., pp. 242, 243.

<sup>&</sup>lt;sup>8</sup> Waagen's parallel series end in the evolution of identical forms or species from or through different species. We have never met an example of this kind which did not admit of explanation as the result of migration. Waagen's remarks, however, apply to parallel series in general, whether the forms ultimately evolved are the same, or merely resemble one another more or less closely.

We reproduce this conclusion in full, though, as may be seen by reading the preceding pages, we differ essentially as to the causes that produced parallelism between different series in the same or different localities. Nevertheless, Waagen agrees with us in rejecting the doctrine of natural selection as a fundamental cause of parallelism, and has also stated in 1875, from independent observations, the possibility of doing what we have been putting in practice ever since 1866; namely, predicting what sort of species would be found as descendants of certain given forms, and then subsequently finding them. This experience has also been shared by Professor Cope, who makes similar statements of his own observations among fossil and recent Batrachians and Reptiles. The method pursued by both of us differs from that ordinarily used by naturalists in predicting the existence of new forms, in that it relies upon the action of the law of acceleration, and the constant recurrence of similar forms in different series of the same stock, or, as we have explained above, upon the law of morphological equivalence.<sup>1</sup>

## Theory of Radicals and Morphological Equivalence in Retrogressive Forms.

There are certain species among complicated acmic forms which became the ancestors of uncoiled degenerate series, that can be properly termed nostologic forms on account of their complete reversion to the uncoiled forms of the radical groups among Nautiloids. These were not confined to any special class of forms, though more frequent among the higher than among the trunk stock of radical forms. They are what we have called geratologous radicals. Thus Lobites of the Trias must have sprung from some geratologous radical among the Goniatitinæ; and Hauer's Cochloceras with its turrillites-like whorls, and the straight Rhabdoceras, both have sutures which indicate derivation from some genus like Helictites or Choristoceras among Ceratitinæ of the Trias, ribbed shells with very simple sutures.<sup>2</sup> Choristoceras, also, had discoidal species in the Rhætic beds.

We treat these forms as probably degradational, because of their simpler ornamentation and sutures, and also because the similar uncoiled shells among Gasteropoda and among Ammonitinæ may be followed until they grade into closely coiled and more complicated shells, from which they probably arose.<sup>3</sup> The geratologous forms have a most important bearing on the conclusions reached in this essay. They terminate the geologic history of their suborders, just as the Turrillites and Baculites, and others, appear as the final forms of Ammonitinæ. They were also coextensive with the existence of the cephalopod type, and were evidently liable to be evolved at any time in their history, and to increase in

<sup>&</sup>lt;sup>1</sup> The law of acceleration and of morphological equivalence has been stated in the Preface, pp. iv. and v.
<sup>2</sup> These lines were written before Zittel's superb work, "Handbuch der Paleontologie," had appeared, in which (p. 431) he associates these forms in exactly the same order. Although his text does not allude to the genesis of the forms, his mode of arrangement shows that he probably had the same idea in mind.

<sup>&</sup>lt;sup>8</sup> Parallelisms of Individuals and Order among Tetrabranchiate Mollusks, Mem. Bost. Soc. Nat. Hist., I., 1866-67, and Proceedings of same, I., 1866, p. 302. Genetic Relations of Stephanoceras, Proc. Bost. Soc. Nat. Hist., 1876, XVIII. p. 380. Also Genesis of Tertiary Species of Planorbis at Steinheim, p. 8.

numbers whenever conditions became unfavorable to the evolution of normal progressive forms. The degenerative nature of the uncoiled Ammoniting and Lytoceratinæ of the Cretaceous has been very generally recognized. They were regarded as diseased forms by Von Buch and Quenstedt, and Neumayr's discovery of the prevalence of simpler sutures even in the normal forms of the Cretaceous has completed this wonderful picture of wholesale degradation. It can be confidently stated, that the well known cretaceous genera of uncoiled shells, Crioceras, Ancyloceras, Ptychoceras, Hamites, and Baculites, are the morphological equivalents of similar forms occurring earlier in the Jura, but that they are not their lineal descendants. The series of Cosmoceras (Amm.) bifurcatum worked out by Quenstedt, and studied also in detail by the author, had shells which became gradually uncoiled. Quenstedt named the uncoiled forms Hamites, but has correctly traced them to the coarsely tuberculated species Cos. bifurcatum. There is also a finely tuberculated specimen, baculatus, with a broader abdomen, which does not otherwise differ from bifurcatum. To this last he is disposed with good reason to refer an arcuate and a straight baculiteslike shell. This same tendency is observable among the shells of the Planorbidæ at Steinheim.2 Among living shells of a closely allied, if not identical, species of Planorbis at Magnon,<sup>3</sup> similar but exaggerated and evidently diseased forms occur, and the physical conditions are such that we can attribute the tendency to the unfavorable and abnormal nature of the surroundings.

We have previously pointed out, that such uncoiled shells could not have had the same habits as closely coiled ones. The appearance of a rostrum in the Ammonitinæ indicates that they had become exclusively crawling animals, in consequence of the disappearance of the ambulatory pipe or hyponome. In the shells of uncoiled Ammonitinæ the rostrum though smaller is still present. Scaphitoid, ancyloceratoid, hamitoid, and ptychoceratoid shells, to whatever genera they may be eventually referred, have one peculiarity in common, the living chamber is bent backwards, forming a shepherd's crook. The absence of the hyponome and the presence of the rostrum in these forms show that they could not have been swimmers, like the modern Nautilus with its large hyponome and corresponding sinus in the aperture and in the striæ of growth along the outer (ventral) side of the whorls. The shepherd's crook added to the rostrum in the living chambers of the shells mentioned above indicates not only a wide departure in habits from the close-coiled Nautiloids, but also from the close-coiled Ammonitinæ, since such creatures could not have crawled with facility. They must have been stationary, either hanging among the branches of plants and feeding upon them, or living with their lower portions buried in the ground and cleaning the surrounding surfaces for their food. Other suppositions might be made, but all hypotheses would involve a wide departure from the habits of their immediate ancestors, and from those of their morphological equivalents, Lituites, Gyroceratites, or other uncoiled Nautiloids, none of which have the reversed shepherd's

<sup>&</sup>lt;sup>1</sup> Der Jura, p. 400, plates lv., lxxii.; Amm. Schwab, Jura, p. 576, plate lxx.

<sup>&</sup>lt;sup>2</sup> Gen. of Plan. at Steinheim, Summ. Pl. ix.

<sup>&</sup>lt;sup>3</sup> Ann. Soc. Malacol, Brussels, VI., 1871, Planorbis complanatus (forme scalaire), by M. Lois Piré.

crook in the living chambers or the rostrum. These cases also illustrate Dohrn's theory of change of function, and the effects produced upon organs thereby, which has been of the greatest use in our researches. Semper's researches and experiments explain changes in organisms in the same way, as probably caused by changes in the surroundings which have led to the adoption of new habits, and the consequent modification or suppression of already existing organs, and sometimes to the building up of entirely new organs or parts. It is interesting to note, that our investigations, though necessarily confined to purely morphological phenomena, have led to theoretical results similar to the conclusions of Dohrn, Semper, and others.

We can account for the existence of the parallel series on the basis of the following law of relation to the surroundings:

The response or reaction of the forms of different series to the action of the ordinary surroundings in the same habitat produced progressive morphological equivalence, when the external influences were favorable to growth.<sup>3</sup>

The environment may assuredly be assumed to have been favorable in the case of the parallel series of normal forms of the Ammonitinæ and other chambered shells, whether occurring in India or Europe. The diversity of these causes was very considerable, but it was not of such a nature as to imply a change of habitat, or any fundamental change not favorable to the growth of the shell. The average size of Goniatitinæ is considerably below that of the Ceratitinæ, and these in turn, as well as the Lytoceratinæ and Ammonititinæ of the Trias, are smaller as a rule than the same suborders during the Jura and earlier Cretaceous. The steady increase in size in all the progressive series of the Arietidæ culminating in the huge shells of Coroniceras shows this very plainly, as may be seen upon consulting the Summary Plates, and the same is true of Planorbidæ at Steinheim.

When the environment, however, became unfavorable to growth, we find retrogression and retrogressive equivalence. Lobites is a genus of small species; Choristoceras, Cochloceras, and Rhabdoceras are also smaller than most of the Ceratitine. The deformed species of the bifurcatus series are smaller than the normal bifurcatus. All of the scaphitoid shells are notably smaller than their congeners, and though there are many large Crioceratites, Ancyloceratites, and Baculites, there are, so far as we know, no exceptions to the rule in cases which have been traced to close-coiled forms. Retrogression is also exhibited in the decreasing size of the retrogressive forms of Agassiceras, Asteroceras, and Oxynoticeras.

In the pathological species with extremely retrogressive forms there is an evident exhaustion of the normal powers of growth and development, and premature senility. This is shown in the uncoiling, destruction of the ornaments, and often also by the retention of næpionic and nealogic characteristics in adults. The form and sutures of straight shells in the Jura and Cretaceous, for example,

<sup>&</sup>lt;sup>1</sup> Der Ursprung und der Princip des Functionswechsel, Leipzig, 1875.

<sup>&</sup>lt;sup>2</sup> Wachsthum's Beding. d. Lym. stagnalis, Verhandl. d. Wurzb. phys. med. Gesell. N. F., IV.; also Naturl. Existenzbedin. d. Thiere, Leipzig, 1880; and Animal Life, etc., Appleton's International Scientific Series, 1881.

<sup>&</sup>lt;sup>3</sup> See also Preface, pp. iv. and v.

differ but little at any age. The four or six lobes of the young are retained throughout life, and have comparatively simple margins. The adult, however, is not similar to a true larval form except in the same sense that an old whorl is similar to its own young, or the toothless gums of an old man are similar to the same parts before the teeth appear. The Baculites are not as a rule strictly tubular whorls, as in the næpionic stages of other Ammonitinæ, but are generally more or less compressed in the adults, like the aged whorls of close-coiled shells. The development skipped the normal progressive stages of the proximate close-coiled ancestors, and, like syphilitic children, these shells had no proper adult stages, but assumed senile, degradational characteristics while still young, and are, as we have said above, purely nostologic forms.

The law of evolution for geratologous forms seems therefore to be as follows:

The response or reaction of the forms of different series to the action of the ordinary surroundings in the same habitat produced retrogressive morphological equivalence, when the external influences were unfavorable to growth.

We cannot account for the number of uncoiled Ammonoids in the Upper Cretaceous, their wide distribution, and the undeniable fact, that they were the members of an order then rapidly nearing extinction, unless we imagine the general conditions of life during this period to have become unfavorable. The unfavorable causes produced in the forms of the groups as a whole similar modifications to those caused by the unfavorable effects of the local surroundings in Cos. bifurcatum, and other shells in more limited localities during the jurassic period.

The bifurcatus shells and the uncoiled cretaceous Ammonoids are not isolated individuals,—like the turrillitic deformities of Ammonitinæ figured by D'Orbigny under the name of Turr. Boblayi, Valdani, and Coynarti, or the planicostan deformities figured in Cor. rotiforme, Plate III. Fig. 7–13, and the scalariform Planorbidæ of Magnon, or multitudes of similar instances known to every student of these fossils,—but series of varieties, species, and genera. These can only be accounted for as the result of hereditary tendencies acting upon races and species, through successive generations, for periods of time more or less prolonged.

The evidence is very strong, that Baculites, Scaphites, etc. of the Cretaceous are not necessarily species of the same genus, but probably always polyphylettic in origin. The Baculites of North America have so close resemblance to those of Europe, that they are usually considered as allied species; but there are indications in the peculiar nodular markings and great size of many species, which lead us to think that they originated from American stocks. Several species of American Scaphites have common characteristics in the sutures, and in the aspect of the ribs and tubercles, and the abdomen, which suggest affinity with Placenticeras. Meek's plates of Scaphites, published in his Invertebrate Paleontology, exhibit common characteristics so far as the sutures are concerned, especially the large size and length of the first lateral lobes, but he gives no figures of the tuberculated young of Placenticeras placenta, which make this comparison closer. The Amm. Mullanus on Plate LVIII. Fig. 1, 1 a, from Upper Cretaceous, Chippeway Point, near Fort Benton, has exactly the form in some

<sup>1</sup> U. S. Geol. Survey of Territ., Hayden, IX., plate xxxiv., and Placenticeras on plate xxiii.

examples; also the sutures, Plate VI. Fig. 9, of the young of *Scaph. ventricosus*, Plate VI. Fig. 7 b, 8–8 b, of the same locality; the pilæ, the involution of the whorls, and the sutures are also similar. It differs only in possessing the scaphitoid living chamber, which is well marked. This group of Scaphites are stouter, and have different sutures from Placenticeras.<sup>1</sup>

In Europe Stephanocerus refractum, the Amm. refractus of authors, is a true Scaphites, but no one thinks of calling it Scaphites, and it is usually referred to the group of normal Ammonitinæ, in common with several other distorted forms. In an article on "Genetic Relations of Stephanoceras," we discussed the affinities of this and similar distorted forms, trying to show the former existence of a general tendency to imitate the scaphitoid mode of growth in Stephanoceras Gervilii, microstomum, and platystomum. These species rebuilt a living chamber at each arrest of growth, which was eccentric, having a flatter curvature, and being smaller than the included whorl. This living chamber was also resorbed at each period of renewed growth, as in Scaphites.

The well known form Amm. vertebralis Sow., of the Upper Jura, was described by Quenstedt as a diseased scaphitoid form, derived from Amm. cordatum, and this conclusion has also been confirmed by my own observations. Stephanoceras bullatum³ has a shell which is precisely like typical Scaphites in the form and aspect of the last whorl, but does not depart from the spiral as in Scaphites. It is, in other words, intermediate between Scaphites and the normal closely coiled Ammonitinæ of the Stephanoceran group. The Anm. microstomus impressæ of the Upper Jura is figured by Quenstedt as a form of Steph. microstomun, to which it has a close similarity, although smaller, and the author concentrates his knowledge of the relation of these forms in one sentence, "Scaphites sind haufig nur kranke Ammoniten,"—Scaphites are often only diseased Ammonites. This statement, which was also Von Buch's opinion, requires a qualification, since they are not simply sick or diseased Ammonids, occurring sporadically like occasional distortions, but races or stocks with cataplastic tendencies inherited and increasing in successive generations.

The distribution, affinities, and cataplastic nature of these forms indicate local origin, but during the cretaceous period unfavorable conditions prevailed so generally that series of them were produced independently, and apparently simultaneously, in many localities in Europe and in this country. Thus, equivalent series of nostologic forms, like Scaphites, Ancyloceras, and Baculites, arose in groups of species, which were not genetically connected with one another, but more or less closely with widely separated and distinct genera of the progressive Ammonitinæ and Lytoceratinæ.<sup>4</sup>

<sup>3</sup> Die Ceph., p. 61.

<sup>&</sup>lt;sup>1</sup> These remarks, however, are considered to be simply suggestions, which the author purposes to follow out and publish with proper details.

<sup>&</sup>lt;sup>2</sup> Proc. Bost. Soc. Nat. Hist., XVIII., 1876, pp. 370-384.

<sup>&</sup>lt;sup>4</sup> Zittel, in his admirable "Handbuch der Paleontologie," I. pp. 440-446, adopts Neumayr's opinion as to the connection of the typical cretaceous genera of Hamites, etc. with the Lytoceratinæ, founding his belief in their genetic connection upon the sutures and smooth shell. On pages 481, 482, he confirms Neumayr's and Uhlig's opinion of the variety of genera from which the more ornamented shells of Ancyloceras, Crioceras, etc. had been derived.

Neumayr was the first to trace systematically the uncoiled forms of the Cretaceous to several groups and distinct species of normal close-coiled Ammonitine, thus confirming Pictet's isolated but suggestive observations on Acanthoceras angulicostatum, and declared that Acanthoceras, Olcostephanus, and Hoplites were the radicals of the uncoiled forms previously included under a number of generic names by D'Orbigny and other authors, and also traced the genera Hamites and Turrilites to an origin in Lytoceras. Uhlig 2 holds views similar to Neumayr, tracing most of the Crioceratites to Hoplites, but considers that Olcostephanus, Acanthoceras, and Aspidoceras had also crioceratitic derivatives. Our conclusions, therefore, are in accord with the results of the researches of Quenstedt, Neumayr, and Uhlig upon the same class of forms.

The Ammonitinæ of the Lias and Oölites in extreme old age, as a rule, lost the tubercles, pilæ, and often the keel, the whorls became smooth, and decreased in size, tending to take on a rounded or triangular outline in section, according to the group in which the species belongs. Thus, in Plate I., Fig. 24 and 25 show the changes which took place in the old whorl of Cal. raricostatum, and Fig. 1 and 2 the similar effects in the old age of Cal. carusense. The whorl in both became rounded, and lost its ribs, etc. On Plate V. Fig. 8, 9, may be seen the old age of Cor. Gnuendense, and on Plate VI. Fig. 1, 2, the similar old age metamorphoses of Cor. trigonatum. In these last the quadragonal whorl of the adult became trigonal, instead of being rounded by senile degradation as in the first instance. On Plate X. Fig. 1–3, there are illustrations of individuals of Ast. obtusum, which can only be accounted for as the results of premature old age in this species, since the young until a late period of growth are identical, and both Professor Fraas of Stuttgardt and the author have identified them under this name.

These changes are all due to the loss of power in the old animal, which can no longer maintain its normal rate of increase in size as it grows. Thus the smaller discoidal whorls of Caloceras with low keels became rounded, and the quadragonal whorls of the keeled and channelled Coroniceras became trigonal. The latter is really a stage of reduction in size, intermediate between the quadragonal form and completely degenerate rounded whorl of extreme age, but, so far as is now known, this last stage was not reached by the progressive forms of the Arietidæ except in Oxynoticeras.<sup>3</sup>

Notwithstanding the evident loss of power, and the consequent and well marked changes taking place in the old whorl of many species of Vermiceras,

 $<sup>^1</sup>$  Zeits, deutsch, geol. Gesell., 1875, pp. 874, 875, 924, 935, and subsequently with Uhlig in Paleontogr., XXVII.

<sup>&</sup>lt;sup>2</sup> Denksch. Acad. Wien, 1883, XLVI. p. 258.

<sup>&</sup>lt;sup>3</sup> One of the finest illustrations of the effects of senility upon the shells of the Ammonitinæ of the Jura is given by Waagen (Geol. Surv. of India, Ceph., Jurass. Fauna von Kutch, pl. xi. fig. 1). In a large specimen of *Perisphinctes aberrans*, the old whorl became smooth, greatly reduced in size, rounded, less involute, and finally exhibited a series of heavy folds on the sides. These senile folds are also common in the old of many forms of the Upper Jura, but are rarer and smaller in the Oölites and Lias. They may be due to prolonged arrests of growth, and the decline of the power to resorb the thickened edges of the apertures, after each period of rest. But, whatever the cause, they certainly indicated a loss, not an increase of strength. This is shown by the degradation in size and form of the whorls in such examples as are given below in the descriptions of *Cor. Bucklandi*, *Cor. trigonatum*, *Ast. obtusum*, and especially *Oxyn. Lotharingum*.

Coroniceras, and Asteroceras, the stages of decline in individuals are not usually attended by such complete metamorphoses in these normal progressive forms as in Oxynoticeras and many others among the jurassic Ammonitinæ. The keel persisted, and is generally still visible even in extreme age, though often greatly reduced in size; the whorl also usually continued the same rate of growth so far as dorso-abdominal diameter is concerned. It therefore appeared to increase in size throughout life when viewed laterally, even in very large individuals of Vermiceras, Coroniceras, and Asteroceras. It is to be anticipated, in some very rare cases of exceptional longevity even in these species, that the keel would be absent and the whorl would become rounded. This happened in senile specimens of Oxyn. Lothwingum, which apparently possessed less power of resisting the effects of extreme age. This is a very interesting fact, since Oxynoticeras is the paracmic series of the Arietidæ, and according to our views would be likely to exhibit strongly marked degradational characters.

It is obvious that the decrease in the size of the whorl, if continued long enough in old age, must have finally caused the last whorl to strike off from the regular line of the spiral, as in the Crioceras. We searched the collections of Europe during the year 1873 for a specimen of a normal species of large size and sufficiently advanced in age to refute or confirm this view, and finally found one, through the aid of Professor Mösch, in the Museum under his charge at Zürich. This was a large fossil of the Neocomian from Sentis, in which the adult whorls were ribbed, but the outer whorl old, smooth, and contracted to such an extent that at a short distance from its termination it was separated by a distinct gap from the abdomen of the next inner whorl. Professor Mösch was impressed by this fact, and gave this specimen, which he considered a new species, the manuscript name of Amm. (Scaphiles) umbilicus, which it probably still retains.

I have examined all the figures of M. Barrande, anticipating the finding of some marks of senility in individuals among the lower types of Nautiloids, and have not been disappointed. M. Barrande classifies the form of the siphon as "the cylindrical, the nummuloid, and the mixed"; and though he nowhere, so far as I can find, describes these metamorphoses of the siphon as stages of development, yet this was probably his real view, since in all his figures, sufficiently complete to show the young, when the siphon is nummuloidal in the adult it is cylindrical in the young.\(^1\) Barrande's figures also exhibit clearly the degradation of the nummuloid siphon, and its return during old age to the cylindrical form;\(^2\) but I cannot find that this eminent author regarded these metamorphoses as having been caused by senility.

<sup>&</sup>lt;sup>1</sup> Phrag. simplex, pl. xix. fig. 9, Gomph. Belloti, pl. xxxii. fig. 6, Phrag. perversum, var. subrecta, pl. c. fig. 11-17, Cyrt. Logani, pl. clxxxii. fig. 2-10, and Cyrt. indomitum, pl. clxiii. fig. 5, all show the development of the nummuloid siphon from the smaller cylindrical tube of the young, or else it has a lessened diameter approximating to the cylindrical condition in the young.

<sup>&</sup>lt;sup>2</sup> Cyrt. rebelle, pl. clxiv. fig. 7, exhibits the change during growth of the siphon, which transforms it from a nummuloidal to a cylindrical tube, and causes the shifting of the position from close proximity to the convex side to near the centre of the last formed septum. Orthoc. docens, pl. ccl. fig. 7, exhibits a similar series of metamorphoses, but the siphon remains at the centre of the whorl.

Degradation in the ornaments, markings, etc., occurred, but is less marked and rarer on account of the frequent absence of the shell. Prof. James Hall has figured cases of senile degradation in Orthoceras, and we have ourselves seen several similar examples.

We have not been able to trace any remarkable changes in old age among the silurian, devonian, or carboniferous goniatitinæ. The dyassic and triassic forms of Ammonoidea with highly ornamented shells have not, as far as known, exhibited cases of senile metamorphosis in any noticeable abundance, and there is a marked absence of these in Mojsisovics's plates, although a few are figured.

There is an easily observed increase in the effects of old age upon the last whorls of the shell in the Jura. Every group, however, does not show the effects of senility equally. There are not only less remarkable metamorphoses in the radical genus Psiloceras, but also less in the Arietidæ, as a whole, than in the Ammonitinæ of the Upper Jura. This retrogression correlates directly with the increasing prevalence of geratologous uncoiled shells in the Cretaceous. There is, therefore, among Ammonoidea a general progress up to the Jura, which is definitely expressed in the life of the individual as well as in the life of the type, and a general decline in the later Jura and Cretaceous, which is also definitely expressed in a similar way. Geratologous types and forms are also less frequent among the paleozoic and earlier mesozoic than in later mesozoic series. Individuals apparently had greater strength as individuals in these earlier periods, senile metamorphoses being less marked in their old age. The phenomena presented by radical types also accord with this statement. If we pick out those types which were the progenitors of series, they appear to have been less affected by degradational changes than the more specialized forms which arose from them. This fact, however, as we have often stated, corresponds directly with the more complicated organization of derivative forms, as contrasted with the simpler structures of radical forms. There are more characters introduced in the adults of specialized derivatives, and the necessary disappearance and degradation of these marks the old age of the individual in such types with more obvious modifications.

As we have stated above, however, geratologous metamorphoses do occur even in Orthoceratites, and series of Nautiloidea. The Lituites of the Phillipsburg (Canada) and Fort Cassin limestones,<sup>2</sup> which we are now studying, and the Lituites and Trocholites described by Holm,<sup>3</sup> have in their youngest stages forms which indicate derivation from nautilian shells, thus proving that they are not radical forms, but degenerate uncoiled derivatives of prepaleozoic or paleozoic stocks of close-coiled Nautiloids, of which they are the last survivors. Trochoceran species belong to several different genera, and are all degenerate forms.

<sup>&</sup>lt;sup>1</sup> Orthoc. fusiforme, figured in Nat. Hist. of New York, Paleont., I., pl. xx. fig. 1, is a very large specimen, with the last three sutures nearer together than the preceding, and this generally indicates advanced age among Ammonitinæ. The increasing width between the folds in the shell of Orth. crotalum, Hall, Paleont., V., pt. 2, pl. xliii. fig. 1, 2, 6, though characteristic of the living chamber, as described by him, probably became permanently characteristic of the senile stages. Very large specimens of Endoceras not infrequently show approximation of the sutures and less distinct annulations than in the adult stage, though this does not appear to be an invariable accompaniment of age, as in the Ammonitinæ.

<sup>&</sup>lt;sup>2</sup> Whitfield, Bull. Am. Museum, New York, I., No. 8.

<sup>&</sup>lt;sup>3</sup> Dames et Kayser, Pal. Abh., III., pl. i. and v.

Ascoceratites, Discoceratites, and Ophidioceratites also indicate lost faunas, in which such types had their now unknown, but progressive progenitors.

Notwithstanding, however, these geratologous series and the facts already stated, the shells of the surviving stocks of Nautiloidea were not usually so perceptibly changed in old age as the more specialized shells of Ammonoidea. So far as known, the shell of a nautiloid, whether fossil or recent, though it may lose tubercles and perhaps become somewhat changed, neither becomes very decidedly depressed nor decreases perceptibly in the involution of its whorls during old age. This remarkable exhibition of persistent growth force in individuals, when taken in conjunction with the slight senile metamorphoses of the smooth radical types of the Ammonoidea and the persistence of the keel in the normal progressive forms of the Arietidæ, the persistence of Nautiloidea until the present time, and the absence of nostologic series in Nautiloids of the Mesozoic and Neozoic, all show how complete is the correspondence between the ontogeny of individuals and the phylogeny of the groups to which they belong.

Alcide d'Orbigny drew attention to the old age of the individual among Ammonitinæ in his "Paléontologie Française." He divided the life of the individual into five periods, distinguishable from each other by the external characteristics of the shell; namely, the first period, or "période embryonnaire," during which it is smooth and the abdomen round; the second period, or "première période d'accroissement," which is marked by the advent of the tubercles, or ribs and keel, if there are to be any upon the adult shell; the third period, or "dernière période d'accroissement," during which the tubercles or ribs and the keel are fully developed, and the whorl takes on its adult configuration; the fourth period, or "première période de dégénérescence," during which the ribs or tubercles begin to separate more widely and become depressed; and the fifth period, or "deuxième période de dégénérescence," when all these ornaments are obsolete, and the exterior is smooth again as in the young.

The recapitulation in which he sums up the results of this remarkable series of observations is equally truthful and instructive. The following paragraph conveys the sense of the original, though its piquancy and force is lost in translation. "These modifications are not due to chance, but to decided regularly occurring periodical metamorphoses, which affect the larger number of the Ammonites, and which invariably operate in a regular order of succession. In fact, each one, though smooth in the youngest period, covers itself at a later time in the course of growth with tubercles around the umbilicus, afterward with ribs, striations, or tubercles upon the back (abdomen). It is then in the adult stage. Having arrived at the maximum of external complication, all of these ornaments begin to show signs of alteration; it (the shell) degenerates; its striations and dorsal (abdominal) ribs first disappear; then follow its lateral ribs or tubercles, and in old age it becomes fully as simple externally as it was during the embryonic period." 1

<sup>&</sup>lt;sup>1</sup> There are apparent exceptions to this law, as observed above, in the heavy folds of the senile stages of many forms in the Upper Jura, and some in the Lower Jura. The young of these forms, which have not yet been investigated closely, will, however, probably explain this discrepancy by showing that the senile folds correspond with larval folds, as is the case in Oxynoticeras of the Lias.

The accomplished author of the "Paléontologie Française" denied that the internal parts were affected by old age, "ne montrent qu'une complication toujours croissante et jamais de dégénérescence." This error was corrected by Quenstedt who pointed out that the closer approximation of the sutures in large individuals was due to senility, and the author is now able to record that he has either observed or seen figured similar cases of approximate sutures, indicating senile degradation in all of the different forms of chambered shells, except in Belemnoids, which have not yet been investigated.

D'Orbigny and Quenstedt were both satisfied with noting the details of the old stage in the individual, the diseased aspect of certain forms, and their reproduction of the characters of their own young and of those of older forms, but did not attempt to explain the wider meaning of these parallelisms. In former papers we have asserted that the close similarity between the smooth, straight Baculites of the Cretaceous, the extreme nostologic form of the Ammonoids, and the smooth, straight Orthoceras of the Cambrian, the common radical from which both Ammonoids and Nautiloids sprang, is parallel with the resemblances which exist between the nostologic or oldest stages of the individual and its own young.

This resemblance between radical and geratologous forms in smaller groups, like the Arietidæ, was slighter, and often consisted merely in the smoothness of the shell, or loss of the keel, or decrease in the amount of involution of the whorl. Ast. Collenoti and Psil. planorbe both have the compressed helmetshaped outline of the whorl in section, and are smooth, though Collenoti exaggerates this form, or is more involute and flatter than planorbe. The most remarkable cases of geratologous reversion in the Lias are found in Oxynoticeras Lotharingum, in which the old whorl loses its keel, and exactly reassumes through degeneration the compressed helmet-shaped aspect of the adults of Psil. planorbe. Even this extreme example among Arietidæ, however, is not in any sense an uncoiled shell. It is very nearly a complete parallel with the smooth keelless proximate radical form Psiloceras, and may therefore be termed a nosologic species. It barely attains this extreme rank in degeneration, whereas other species, such as Ast. Collenoti, which retain the keel and do not decrease in size of whorl, are only clinologic approximations.

The resemblances which occur between the young and old of the same individual in the same parts and organs take place because the organs lose their power to exercise the functions which distinguished them in the adult, and becoming useless, are either partly or wholly atrophied and resorbed.

## THE THREE MODES OF DEVELOPMENT.

The likeness between the younger stages of growth and the senile stages of decline in the same individual is, as we have just shown, due to the disappearance in old age of the specialized ephebolic characteristics acquired in the progressive nealogic and adult stages of growth. In groups the resemblances between radical and geratologous forms is occasioned by a similar suppression in

the latter of the more specialized ephebolic characteristics which arose in the group during its acme of evolution in time.

We now propose to take one step more, and try to show that this tripartite correlation in the development of the individual and in the evolution of the type correlates with a similar cycle in the modes of development of the individual, which we have classified as the direct radical, or anaplastic mode, the complex, or metaplastic mode, and the direct geratologous, or cataplastic mode. We are thus carrying to definite conclusions and confirming by application the laws announced by Haeckel in his "Morphologie der Organismen," and by the author independently with regard to the ontogeny of the Cephalopoda, in his essay on the "Parallelism between the Individual and Order in Tetrabranchiate Cephalopods." <sup>2</sup>

Haeckel was a strong advocate of the general efficacy of natural selection as a motive force of far greater importance in the evolution of types than has been granted in this and other publications by the author, and did not give as much weight to the correlations between the ontogenetic and phylogenetic cycles. If these have the correlations here claimed, then we can see that a theory like that of natural selection, which does not recognize the action of some law which has affected both the individual and the type in the same way, cannot be reconciled with the observed facts in the evolution of forms. A theory of evolution must necessarily, while admitting the origin of new characters by external causes, also recognize the limitations due to the force of heredity in conserving the type. It must admit fully the plasticity of organisms, and the power of external conditions to effect fundamental changes in structure by means of internal reactions, that is, through the action of either conscious or unconscious effort, - but not deny to heredity its fullest effect in the tendency of like to produce like. It should emphatically deny that heredity tends to produce like with variations, or that there is any such thing as a tendency to variation which is inherent and not produced by external forces. It must recognize not only the three physiological phases of epacme, acme, and paracme, but that all the phenomena of evolution accord with this cycle. It should show that not only the general physiological phenomena, but also the relative strength of the individual, as testified by the slight effect of old age upon the shell in the oldest and simplest types, and the more rapid evolution of paleozoic as compared with mesozoic types, and of geratologic types at the termini of each special group of forms in time, are strictly in accord, and testify to the existence of a common law governing and producing cycles. It must also recognize that there is a growing stability in types, and less important structural variations at the acme of a group than during its epacme or paracme; and that its habitat was freer at first than it was subsequently during its acme.3 The struggle for existence between species, if there were any at first, (which we do not believe,) must have been very slight compared with what it became during the crowded acme, and

<sup>&</sup>lt;sup>1</sup> Vol. II. pp. 18, 22, 320.

<sup>&</sup>lt;sup>2</sup> Mem. Bost. Soc. Nat. Hist., I. p. 195 et seq., and Proc. of same, X., 1866, p. 302.

<sup>&</sup>lt;sup>3</sup> See Genera of Fossil Cephalopoda, p. 261, and Fossil Cephal. Mus. Comp. Zoöl., p. 339.

this shows conclusively the comparatively small influence of natural selection except during the acme of groups.

Another series of facts in favor of the views here advocated is to be found in the cycle formed by the modes of development. The more ancient and simpler forms of Cephalopoda, like Orthoceras and most of the earlier forms of Nautiloidea, had a direct mode of development, during which the individual passed through certain well marked changes; but these were less numerous and not so crowded together as in types with more complicated development. The young and adults of the same individual among straight radical shells differed comparatively little in form and ornamentation. The siphon in Piloceras, and in some species of Endoceras, for example, was comparatively little changed in adults from what it had been in the young, and Cyrtocerina as described above, probably remained completely macrosiphonitic throughout life.

When closer coiling was introduced and more concentrated development occurred, as in the higher Nautiloidea and Ammonoidea, we found, as one of the results, the omission of some hereditary stages. As we have said above, the first air-chamber disappeared in Ammonoidea, having become fused with the protoconch, which stage acquired through this earlier inheritance a tendency to secrete a calcareous shell, and in consequence of this fusion the execosiphonula was also carried back and appeared earlier in the life of the shell and animal.

The næpionic or true larval stages, as we have said above, became more accelerated in the angustisellate young of the Lytoceratinæ and Ammonitinæ, and the succeeding or nealogic stages were introduced with a profusion of ornaments and increased complications in the outlines of the sutures, curves of the septa, structure of siphon, increased involution, and changes of structure and form in the whorls, which multiplied the metamorphoses and made the different stages of growth more distinct than in the Goniatitinæ and Nautiloidea.

The complex mode of development of the normal acmic forms, due to the introduction of these new characteristics, is easily perceived in most of the Ammonitinæ, even without breaking down the whorls to examine the young. The ornaments and pilæ on the exposed sides of the whorls show this in most species of the Jura with sufficiently discoidal shells.

The paracmic forms, and especially the degenerate uncoiled species of every group, exhibit a return to the direct mode of development, and a lessening of the variety and number of structural changes. These suppressions became, as we have described them above, so well marked in all the straight baculites-like forms, that a tyro cannot fail to notice the fact. The smooth, slightly compressed whorl retained nearly the same form throughout life, the sutures retained the primitive number of næpionic lobes, and the marginal digitations were comparatively simple even in adults.

Similar phenomena occurred in every group. Thus in the Arietidæ the radical *Psiloceras planorbe* had the anaplastic or comparatively direct mode of development, while the descendent species in both these genera had more complicated, metaplastic transformations, due to the introduction of a quadragonal

form, with keels, channels, etc.¹ The metaplastic mode of development of the progressive forms was again exchanged in the still higher and more specialized but degenerate and geratologous forms, like Ast. Collenoti and the Oxynoticeran series, for the cataplastic mode. The young more closely resembled the later stages, and passed into them with less abrupt transitions, because of the action of the law of acceleration, and the consequent omission of ephebolic characteristics. The same process took place in each genus of the Arietidæ, more or less according to its place in the cycle, and in our descriptions of the species and series the evidence will be given.

#### LAW OF ACCELERATION.2

Whenever the character or form, whether healthy or pathological, became fixed in the organism, it became at the same time subject to the law of acceleration. Its previously transient and sporadic appearance ceased, and a series came into being having this character, whatever it might be, constantly reproduced in earlier stages of the species.

The fixity of many characters on first appearance may be reasonably doubted, but not their subsequent tendency to acceleration. The hollow keel of Oxyn. oxynotum is a novel character, and it seems to be present in every mature specimen of the species. Nevertheless, in this and in all cases like this, there is a dearth of evidence of a positive nature, and some specimens may yet be found which did not possess it. There are however, examples without number like the variable first appearance of the abdominal channel in Schlotheimia, of the keel in Caloceras, and of the pilæ in Arnioceras and Agassiceras. The young had fold-like pilæ in Schlotheimia, which crossed the abdomen. The single channel which was subsequently produced is a progressive stage, arising partly from the suppression of the folds along the median line, and partly from extra growth of the pilæ on either side of the abdomen. Sometimes the suppression of the pilæ along the median line of the abdomen never took place, the abdomen remaining completely pilated throughout life. This occurred as a sporadic or varietal ephebolic character in Schlot, catenata, but in the higher, later occurring, and more

<sup>&</sup>lt;sup>1</sup> See Chapter III. of this memoir.

<sup>&</sup>lt;sup>2</sup> I have used the term Law of Concentration in several recent essays, instead of, as formerly, "Law of Acceleration," because my attention had been attracted to phenomena which showed that an animal having accelerated development of characteristics did not necessarily have a quick development, but on the concerned, even more slowly than others of its own group. It became essential, then, to get rid of the impression, which I had held in common with some other embryologists, that an animal which skipped many characteristics of its ancestors, or of its own type, had necessarily a quicker growth and development. Undoubtedly, in many instances, especially where acceleration is due to pathological causes, such is the result; but this does not occur in all cases, or perhaps necessarily in any case. In trying to introduce this idea I went too far, and in substituting the term "Concentration" for "Acceleration" made a change which was not an improvement. In this memoir, therefore, I have returned to the older and more appropriate term which stands at the head of this section. The term "abbreviated development" is often used, as it has been by Balfour, for extreme examples of acceleration, and it also implies no necessary relation of time. This term, however, was not invented to express a law of development, and its author did not take into consideration the fact, that such cases are only the extreme expression and the necessary result of a universal law of organic evolution.

compressed, involute forms like Schlot. Charmassei, the suppression, so far as we know, always occurred in normal forms at some nealogic stage, and the presence of a channel is constant even in the young. If the pile again crossed the abdomen, thus obliterating or obscuring the channel, during the life of the same individual, it occurred as a degradational character in the senile stages. Extreme cases of degradation in species did not occur in Schlotheimia, but if there had been any such nostologic forms, they would have inherited this tendency to obliterate the channel during the nealogic stages. The law of acceleration of development was quite as effective in its action upon geratologous as upon progressive characters, as will be seen when we treat of this class of characters farther on.

Besides the examples given above of the inheritance of characters in larger and smaller series, we add the following in order to make our meaning still clearer. The form, shape, and characteristics of the secondary radical, *Psil. planorbe*, are prominently shown in the young of Arnioceras, Plate II. Fig. 10–15, and in the Embryology of Cephalopods, Plate II. Fig. 9, 10, until a late period of the growth of the shell, but are less noticeable in the young of the descendent species, *Cor. kridion*, in which indeed they are perceptible only in the transition form between this species and *semicostatum*. Most of the specimens have young like that figured on Plate III. Fig. 2, and are stouter than the flat discoidal *Psil. planorbe*. These and the young of other species of Coroniceras inherit the stouter quadragonal whorl and peculiar ribs and tubercles, the keel, and the channels, at earlier stages of their growth than those in which they first appeared in ancestral shells, as may be seen by comparing *Arn. semicostatum* with the young of Coroniceras, Plate III. Fig. 19, and Fig. 5, 6, 8–10.

One of the most convincing examples of the law of acceleration which we have studied can be illustrated by using Wright's book, "Lias Ammonites." He shows the latæcostan form of the young on Plate XXXIV., and in Fig. 4-6 the adult of Androgynoceras hybridum, his Egoceras heterogeneum. A more accelerated form is shown on Plate XXXV. Fig. 4-6, in which the young are similar to latæcosta for a less prolonged period of their growth. Wright's Ægoc. Henleyi, Plate XXXIII., is also a specimen of the same species with a prolonged latæcostan stage of growth. Lip. Henleyi, figured by Wright as Ægoc. striatum, Plate XLIII., is also highly accelerated, and most of the specimens have young shells with no traces of their latæcostan ancestry, reproducing only the characteristics of the adult whorls of And. hybridum. Lip. Bechei, also figured by Wright, Plate XLII., is still more accelerated in its mode of development, since the young has no resemblance to the adult of And. hybridum. From the smooth stage of the næpionic period of growth it passes abruptly to a stage in which the shell resembles the adult form of And. Henleyi. The whorls at this stage show the specific characters of the adult of And. Henlevi; they are too involute and too heavily ribbed and tuberculated in proportion to their size to be compared with the adult of And. hybridum.

Würtenberger's book is devoted to the exposition of this law of heredity

1 Paleontological Soc., XXXII., 1878.

among the Ammonites. This author, in his "Studien über die Stammesgeschichte der Ammoniten," <sup>1</sup> traces the Armatus or Aspidoceras stock of the Upper Jura to the Planulati; that is, to the genera Cœloceras and Dactylioceras, which last I had previously described and traced to an origin in *Deroceras Dudressieri* of the the Lower Lias. <sup>2</sup> His work is a summary of evidently extensive observations upon the Ammonites of the Upper Jura, all of which he traces directly or indidirectly to the Planulati. Whether he can sustain this opinion will be questioned by some until he has published his plates. He has, however, studied the series according to proper methods of analysis, and should be given the credit of the doubt. We also, though the author fails to notice the fact, have traced *Pelloceras athleta* to the same species in the Lias, *Amm. annulatus* Quenst., and published the remark <sup>3</sup> that they were genetically connected by intermediate forms. Our observations, therefore, closely accord upon this very important species, and we also agree in the view that most of the jurassic genera we have included in the Spinifera and Plicatifera can be traced to *Cœl. Pettos* as the probable radical.<sup>4</sup>

In his fourth chapter Würtenberger gives the history of the evolution of the Lallierianus series, in which he traces degeneration in the lobes and saddles, showing that changes of all kinds appear first on the outer (adult or senile) whorl of the ancestral forms, and encroach more and more on the inner (younger) whorls in descendants. Neumayr 5 considers that Würtenberger was the discoverer of the law of acceleration in development, and this author states that he first published his new discoveries in "Ausland" of 1873, - about five years after the appearance of precisely similar statements in such scientific periodicals as the Proceedings of the Philadelphia Academy, by Professor Cope, and the Proceedings and Memoirs of the Boston Society of Natural History, by the author. Professor Cope has lately republished his discoveries in a volume entitled "The Origin of the Fittest," and in these masterly essays those who are interested may get a full view of his mode of explaining this law, and will find very complete series of illustrations of the character and meaning of parallel series and other related phenomena.

The decision as to who discovered the law of acceleration is only historically interesting; but it is of general importance that so many persons agree, and that an eminent paleontologist like Neumayr, who has studied such phenomena among fossils, considers the law to be true in its application, as tested by him, with some exceptions. He does not state the exceptions, however, and they cannot be discussed. The opinions of Würtenberger and Neumayr that some species inherited characteristics at later stages than those in which they occurred in any ancestral species or pair, seem at present to rest upon the insecure basis of the apparent need of this assumption in order to account for acceleration as

 $<sup>^{\</sup>rm 1}$  Ernst Gunther, Leipzig, Darwinistische Schriften, No. 5.

Non-reversionary Series of the Liparoceratidæ, etc., Proc. Bost. Soc. Nat. Hist., January, 1872, and Appendix to the same, with a geological table, Ibid., May 20, 1874.

<sup>&</sup>lt;sup>a</sup> Proc. Bost. Soc. Nat. Hist., Appendix to Non-reversionary Series of the Liparoceratide, 1874, p. 33.

<sup>&</sup>lt;sup>4</sup> See above, pp. 23, 24.

E Zeitsch. d. deutsch. geol. Gesellsch., p. 868.

<sup>6</sup> See above, page 28, note 3, and Proc. Bost. Soc. Nat. Hist., 1870, pp. 72, 73.

being due to the law of natural selection. We do not deny the existence of such examples; we are only anxious to hear of their existence, and to be able to examine the evidence.

Weissmann<sup>1</sup> also seems to have been unacquainted with the same literature, and claims the discovery of the law of acceleration for Würtenberger. Weissmann's interpretations of the phenomena were in part very similar to our own. He rejected Würtenberger's theory of the origin of acceleration through the action of natural selection, and states that it is due to the innate law of growth, which rules every organism. In many places he explains this law of growth as a mechanical law, and the origin of variations as due to the innate response of the organism to external forces exciting it to suitable changes. This law of variation through mechanical causation is identical with that advocated by Cope, Ryder, and the author; but with regard to this there can probably be no controversy about priority. Dr. A. S. Packard has shown that such views are essentially rehabilitations and improvements upon Lamarck's theory of effort, and he has appropriately named us the Neo-Lamarckian school.<sup>2</sup>

This eminent author (Weissmann) has apparently abandoned this position in his later works. He claims that the protoplasmic basis of organisms is alone the vehicle of heredity, and substantially imperishable or continuous; that all variations taking place in the organisms, unless they affect this basis so as to modify the ovum, are not inherited; that the variations of males and females are, when inherited in the offspring, the originators of new characters through the new combinations which necessarily arise, and he also regards natural selection as the prime agent in the preservation and perpetuation of these variations.3 We have been unable to find any characters which were not inheritable in some series. The behavior of all characteristics which have been introduced into any series of species shows them to be subject to the law of acceleration, in whatever way they have originated, whether primarily as adaptive characters, according to our hypothesis, or by natural selection and through the combination of the sexual variations, as supposed by Weissmann. All of the degenerative changes took place in retrogressive series, in precisely the same way as is described above for progressive changes. Thus, the degradational characters and uncoiling became noticeable in the old of individuals and of species first, and then appeared, in obedience to the law of acceleration of development, at earlier stages in succeeding or derivative forms, until finally they entirely replaced the normal progressive characteristics of the nealogic stages. A straight Baculites-like modification could not have been produced by the unfavorable surroundings directly from any close-coiled form; it must have arisen from the intermediate arcuate and crioceran modifications. If this be true, heredity must have played its part even in the extreme modifications of abnormal geratologous series, however improbable this may seem.

<sup>1</sup> Studies in the Theory of Descent, Eng. ed., transl. by Meldola, I. pp. 274, 277.

<sup>&</sup>lt;sup>2</sup> Standard Natural History, edited by Kingsley, Introduction; and also Cope's "Origin of the Fittest," in which see index, Lamarck.

<sup>&</sup>lt;sup>3</sup> Continuität der Keimplasmas; also Ueber der Vererbung; see also, as in favor of the views here advanced, Kolliker's criticism, Karyoplasma und Vererbung, Zeit. Wissensch. Zool., XLIV., 1886.

We would also suggest that the phenomena of parallelism, or the evolution of similar forms in different series which can be predicted, is obviously contrary to any law which does not assume that adaptive characters are equally inheritable with differentials. Again, the minuteness and slight importance of some differentials, like the collar of the siphuncle in Ammonoids, which are nevertheless persistent throughout several geologic periods and constant in every series, do not appear to be accounted for by Weissmann's hypothesis. This collar appeared first in the adults of the Goniatine, and became engrafted in the early stages by the law of acceleration, like other characteristics. It should be remembered also that parallel series were continually evolved, while this differential remained comparatively unchanged, and that the alteration of the entire form of the whorl by involution, and the evolution of complicated from simpler radical sutures took place over and over again in different series arising from the same stock. How could males and females have combined to produce similar series of variations, and also unimportant but still persistent differences? How could a characteristic of slight importance to the life of the species have made a deep and lasting impression on the ovum, while others of obviously greater moment to the organism were transient in different series?

There is one phase of the law of acceleration which requires to be dwelt upon as the best means of conveying its full meaning to those not yet accustomed to note its action in their researches. It expresses the mode by which the continual replacement of the older by newer and later acquired characteristics takes place in every genetic series, and therefore explains the mechanism of gradation, whether progressive or retrogressive. Changes in environment, which introduce new adaptive characteristics in the nealogic or adult stages, necessarily add these to the hereditary stages of the younger periods of growth, and thus shorten the development of the latter by direct replacement.

Heredity, as is well known, can continue for indefinite periods to reproduce a useless part or organ, provided it does not interfere with the growth and normal development of useful structures. When interference occurs, as is well known to all physiologists, their resorption is a normal process, due to the fact that they have become through disuse merely passive stores of food for the more active worker cells.

Though species sometimes pass through more than one horizon, they are, as a rule, limited to the levels upon which they first appear. This fact, and the frequent differences in the sediments, which often correspond to differences in the faunas, indicate that the different varieties or species characterizing distinct horizons are more or less directly due to the changes in the surroundings, which occurred in passing from one geologic level to another. We can fully understand the phenomena of acceleration in development only when we begin by assuming that the characteristics last introduced in the history of any type were more suitable to the new conditions of life on the horizon of occurrence of the species, than those which characterized the same stock in preceding horizons. These characters would then necessarily, on account of their greater usefulness and

<sup>&</sup>lt;sup>1</sup> Genesis of Planorbis at Steinheim, p. 28.

superior adaptability, interfere with the development of the less useful ancestral stages, and thus tend to replace them. The necessary corollary of this process would be the acceleration of the previously existing nealogic stages in direct proportion to the number of new characters successively introduced into the direct line of modification during the evolution of a group.

The importance of this law becomes more apparent when consideration is claimed for it as a working hypothesis for the explanation of such obscure problems as occur among insects. The complicated metamorphoses of the Hymenoptera, Diptera, and some Coleoptera, for example, in which feetless and headless larvæ appear, can be attributed to acceleration, like the more normal examples among fossil Cephalopoda. They illustrate the suppression of ancestral thysanuriform stages, which when present in the active larvæ of lower orders indicate that all insects were derived from some ancestor possibly similar to the adult of such forms as Lepisma or Campodea. This gives new interest to the theoretical views of Brauer and Sir John Lubbock, who first pointed out the næpionic characteristics of the adults among Thysanura.

It seems to us equally applicable to the explanation of the medusaless metamorphoses of the fresh-water Hydra, as compared with the marine Tubularia in which the medusa stage is prevalent, and also to the accelerated development of the pelagic medusæ, Geryonia and others, in which the hydra-like stage has vanished.

In Tænia, also, the earlier stages are so accelerated that the secondary sac, furnished with cutting blades, worked by special muscles, and used for digging through the tissues, is still called an ovum by many naturalists, though it is morphologically the remnant of an active form producing the young Tænia by an involution or bud from its walls. The ancestors of Tænia must first have acquired a cercaria or nurse form with cutting blades, and then, the evolution having reached its highest progressive acme, the reverse process of resorption through acceleration began. The constant exercise of the blades by the cercaria and the use of a horny case for the ovum caused these to be retained, while the other characteristics of the cercarian stage disappeared, or else like the blades became more or less fused with the ovarian stages.

Perhaps the most remarkable instance of the loss of progressive characters correlating with a highly accelerated mode of development is man himself; and his example will serve a good purpose in making clear what we mean by a geratologous retrogression, which is often evidently due to a great change in habits, bringing about specialization in certain parts, enlarging and prematurely developing them at the expense of many of the normal progressive characters of the ancestral type. The Caucasian type, in losing the prognathism of the Anthropoids, which is certainly a highly specialized characteristic of the adult forms among the apes, has in a morphological sense made a step backwards instead of forwards. The larger size of the brain as compared with the lower part of the face and jaws is also an embryonic characteristic of all the Vertebrata, even

<sup>&</sup>lt;sup>1</sup> See Cope, Origin of the Fittest, pp. 11, 12, 147, 148, chaps. viii., ix., also Haeckel, Gen. Morphologie, II. p. 446, and Anthropogenie, for similar views.

fishes and birds at an early stage exhibiting this peculiarity. Dr. C. S. Minot has declared, upon similar grounds, that there was nothing in man's structure which justifies us in considering him as morphologically a higher animal than the more specialized Mammalia. Though not willing to indorse this statement as a whole, it is in part true.

Notwithstanding the increased functional power of the brain, the loss of certain characters which once marked the progress of ancestral structures remains to be accounted for. In fact, as suggested by Professor Shaler, the body and its organs exhibit the evidence of having belonged originally to a horizontal type, and in accommodating itself to a vertical position has succeeded in adapting its parts to meet new and more complex conditions, and a new position with relation to gravity, without having made very essential changes in hereditary structures. Man is a walking simian biped, or, as Cope describes him, a "pentadactyle plantigrade bunodont." Nevertheless man is also a highly specialized type. The extraordinary development of the legs, the increased size of the big toe, the differentiation of the feet, the broadening out of the chest and sigmoid curve of the backbone, the differentiation and shortening of the arms, the changes in the pelvis, and other correlative specializations, have probably been introduced through the exercise of the parts in an upright position, as was originally pointed out by Lamarck.

There is, of course, a vast gap to be bridged between man and Oxynoticeras oxynotum, but they are none the less types belonging to the same general category of geratologous forms. They have arisen suddenly, and present alike the commingling of degenerative and specialized characters. Such geratologous species show us that any form having a highly accelerated development, and producing suddenly some new and unexpected characteristics, as, for example, the hollow keel of Oxynoticeras, or the peculiarities of man's structure, may have, in association with these, many retrogressive characteristics.

The extreme example of Baculites-like shells are very distinct from these, and show us that the development of geratologous characteristics may sometimes take place without the introduction of new characteristics. In such cases, the adults may resemble their own young more completely than in man, or in other examples given above, and may be similar in aspect to the primitive radical of the whole group, as is Baculites when compared with Orthoceras. Such considerations and others given above have led us to compare this class of forms in which degeneration is complete with the oldest stage of decline in the individual, and we have accordingly placed them in the same category as nostologic forms. This serves to distinguish them from partially degraded forms, which can be called geratologous, or from forms that resemble the first senile stages of the individual, and can be termed clinologic forms.

In order to account for high degrees of specialization, and their tendency to

<sup>&</sup>lt;sup>1</sup> Amer. Assoc. Adv. of Science, August, 1881.

<sup>&</sup>lt;sup>2</sup> Origin of the Fittest, p. 266, referring of course to the retention in the organization of ancient ancestral characters.

<sup>&</sup>lt;sup>3</sup> Philosophie Zoologique, I., Pt. I., chap viii., Quelq. Observ. rel. à l'Homme.

extreme acceleration in development, the author, in a previous paper,¹ imagined the special means of protection often afforded to the young in such types to be the efficient cause. But the Marsupialia are not the most highly specialized mammals, nor are some of the penguins the most specialized birds, and yet both protect the young in pouches. Distoma and many other parasites are highly protected, and yet in these we find exceedingly long and complicated adaptive series of metamorphoses, with a high degree of protection in some cases, and in others more accelerated modes of development with less protection, as in Tænia. Balfour in his "Comparative Embryology" subsequently adopted the same explanation in order to account for cases of "abbreviated development," some of which he noted, but without, however, recognizing them as due to any general law or tendency of development, or making quotations of Cope's, Packard's, or the author's researches in this direction.

The Diptera and other insects, whose larvæ are placed in protected situations where soft foods abound, and have consequently lost their useless jaws, eyes, legs, and hard chitinous covering, and in some cases even the differentiated segmentation of their ancestral forms, are very remarkable examples of acceleration in development. Doubtless the supply and kinds of food, and perhaps protection, may have had much to do with these changes, as pointed out by several entomologists. The constant correlation of habits and structure in larvæ is, however, independent of protection; and it is evident that such a limited cause could not have produced, as an effect, the universal tendency of acceleration. The hypermetamorphosis of some insects and parasites also shows that protected habitats, or special maternal organs for protection, are not essential to acceleration, since the most complicated and indirect modes of development occur as in Sitaris, where the young are protected during certain stages and unprotected at others.

Acceleration occurs whether an animal is protected or unprotected, whether furnished with one kind of food or another, in all sorts of habitats, and whether it belongs to a progressive or retrogressive series. This can be supported by many examples among recent animals, described by other authors than those specially interested in proving the truth of this law.

With regard to the accelerated forms of shell-covered Cephalopods, they are usually, if belonging to the geratologous category, smaller, narrower, or less gibbous, and sometimes much compressed, as in Ast. Collenoti and in Oxynoticeras, when compared with their immediate progenitors. The more cylindrical whorls of Lituites, Ophidioceras, etc., and the compressed cylindrical forms Crioceras, Hamites, or Baculites, show facts of the same nature. All of these more compressed or more cylindrical shapes were obviously not adapted to the office of accommodating living young; they indicate in a very positive manner that there was less space within their whorls, and consequently less protection for the young, than in the more gibbous shells of congeneric normal forms. It is obvious that no special provision for protection existed for the young in such shells, or in Stephanocera refractum, or Scaphites, which did not also exist in the normal forms with complex modes of development from which they were derived.

<sup>&</sup>lt;sup>1</sup> Genesis of Planorbis at Steinheim, p. 29.

There is also no ground for assuming exceptional protection in the cases of dwarfs, which have accelerated development of retrogressive characters, as, for example, in those of Ast. obtusum, which we shall describe in detail farther on.

### ORIGIN OF DIFFERENTIALS.

Differentials are essential characteristics, which distinguish one group from another, and, unlike morphological equivalents, are apparently directly inherited in successive generations of the series from the distal or proximate radicals. Thus the distinct stocks of the Nautiloids, Ammonoids, Belemnoids, and Sepioids, may be followed without difficulty. The Goniatitine, Arcestine, Lytoceratine, Ammonitinæ, and Ceratitinæ, among Ammonoids, are examples of suborders less easily separated. Vermiceras, Coroniceras, Amaltheus, Oxynoticeras, and Asteroceras are examples of genera affording still greater diagnostic difficulties. In all of these the differentials can with certainty be considered hereditary, since after their introduction in the earlier members of a group they are perpetuated, not only in the earlier species or forms, but more or less even among the most aberrant and geratologous members of the group. Differentials are often described as invariable, but this is an inaccurate expression, which is not in practice trusted by any naturalist of the present time. They are perhaps, when compared with other characters, relatively constant, but in all complete series necessarily pass through stages or phases of evolution. On first appearance, they are apt to be more or less variable within the limits of the species in which they originate, then they become constant in descendent forms of the same series, and finally in extremely geratologous (nostologic) forms they may be in large part or wholly obsolete.

The close-coiled character of the young was certainly a differential among Ammonoidea, but this became constant only in the mesozoic forms. The contraction which marked the tendency to reduce the size of the siphon was not very important at first, and was variable in position among the Endoceratidæ. It was, as has been said, probably fixed at the first septum in Sannionites, and became perhaps invariably fixed at this stage in the Orthoceratidæ, assuming in them the aspect which subsequently also characterized the close-coiled nautilian shells, and the entire stock of the Ammonoidea and Belemnoidea. The contraction in these orders defined or cut off the primitive execum from the parts of the siphon formed subsequently, and its invariable occurrence at one place in the næpionic history of such a vast number of forms is very important in its bearing upon the mode of origin of other and less important differentials.

There is no explanation of the introduction of these characters which permits us to separate them, as belonging to a distinct category, from characters which are adaptive. Nor can we say that any of them more deeply affected the ovum than any other characters. They were simply the earliest in time, and made their appearance in adults first as ephebolic characters, and then as suitable characters were inherited, and, being replaced in due course of time by newer modifications, were gradually forced back through the nealogic stages until they secured representation in the næpionic stages. This seems to be a reasonable

explanation of the observed phenomena; but that the characters, as in Weissmann's theory, singly or in part could have affected the ovum when they first appeared, does not seem to be sustained by the facts. The examples cited above of the transmission of the characteristics of the asiphonula and cæcosiphonula to the typembryo of the Ammonoidea give similar evidence with regard to the origin of embryonic characters, and are directly against Weissmann's position.

Barrande and Munier-Chalmas have tried unsuccessfully to prove the absolute invariability of differentials among fossil Cephalopoda by means of the great apparent differences between the embryos of Nautiloids and Ammonoids, but the discovery of a protoconch in Orthoceratidæ has demonstrated their error, and we confidently anticipate the discovery of some form in which the protoconch will exhibit intermediate characters.

The rostrum in the Ammonoids contrasts decidedly with the central sinus of the same region of the aperture in Nautiloidea, and is a differential of importance, which ought to be mentioned here. The rostrum of the mesozoic forms indicates that the Ammonoids did not possess the ambulatory pipe or hyponome <sup>2</sup> of Nautiloids, which causes the ventral sinus in the aperture and strize of growth in that order. As noted above, they could not have been swimmers in the same sense as the existing Nautilus, and they must have been for the most part strictly littoral crawlers. The habit of crawling as a slower mode of progression combined with varied habitats of shallower waters, may have been the cause of the higher specialization and greater variety of forms and structures which they exhibit. The change from a ventral sinus to a rostrum in the aperture began among the higher Goniatites during paleozoic time, and is shown by the narrower ventral sinus of the aperture, and in the lines of growth on the shell. This sinus also is more distinctly marked, and is present oftener, in the devonian forms of Goniatitinæ than in the carboniferous species.

The Clymeninæ of the Devonian have very small ventral sinuses in many forms, and in others the hyponome may have been absent. The specimens observed by the author have not as a rule exhibited the lines of growth with great clearness, but many of Gümbel's figures give the striations, and in some species they pass straight across the venter. The Ammonoids of the Trias are apparently completely transformed, the rostrum and the ventral saddle in the lines of growth indicating the constant absence of a hyponome.

As the ambulatory hyponome disappeared, all the sutures became more complicated or ammonoidal, and, in correlation with the greater lengthening of ventral and dorsal lobes, the central zone of the septum changed from concave to convex. When one tries to attribute the origin of convexity in the septa, or the multiplication and lengthening of lobes, or the marginal digitations of the sutures among ammonoids to fortuitous variations, he finds at once that their history in the groups of the order is correlative with the phenomena of morphological equivalence. As was long ago observed by Von Buch, and

<sup>&</sup>lt;sup>1</sup> Science, III., No. 52, 1884, p. 126; and also above pp. 10, 11.

<sup>&</sup>lt;sup>2</sup> See Foss, Ceph. Mus. Comp. Zoöl., Proc. Am. Ass. Adv. Science, XXXII., 1883, p. 340; also Science, III., No 52, 1884, p. 123; and above, p. 29.

by several naturalists since his time, the complication of these characteristics increases in each group of Ammonoidea, in strict accord with the amount of involution of the whorls of the shell. The reason for this correlation is easily given. Involute shells have broader sides and must necessarily have a larger number of lobes and saddles, or, if these do not increase in number, then they must necessarily deepen and have more profuse marginal digitations. Origin through fortuitous variation is consequently inadmissible, since one can predict the changes which are to occur under certain specified conditions.

On the other hand, the assumption that these characteristics are advantageous differences, acquired through the struggle for existence, seems to be ruled out by the same facts. Characters and differences which were shared by many series, whether living and contending in the same horizons and localities, or occupying distinct horizons and widely separated localities, must have been due to causes which modified the forms by acting from within the organism. The external causes, as pointed out by several authors mentioned above, could not have had such similar effects, since they were assuredly diverse on distinct horizons and in different localities. The only cause of modification which could have produced similar change in different groups must have been the effortseither as voluntary or involuntary mechanical reactions, or both 1 - of the animals in response to the requirements of the surroundings in the same habitat. As has been said above, all external marks of similar reactions in the animals themselves, such as parallel forms and characters, tend to disappear when the habitat has become changed. That the differentials we have been treating of are of the same nature as parallelisms, in so far as those appearing in one series resembled those appearing in other series, or in so far as they correlate with such characters, will not, we think, be doubted by an experienced observer.

While it is extremely difficult to account for the lengthening of the lobes, or the multiplication of marginal digitations, by means of natural selection, it is not difficult to understand that these complications might have been the result of the habit of holding the comparatively large shell high above the arms. The branching of the posterior ends of the lobes would tend to give greater steadiness of carriage to the shell, and the efforts of the animal to use these organs while crawling would probably tend to increase them in size and length, and in the complication of the outlines. The length of the rostrum was not great in most forms of Ammonoidea, but in some groups it was quite prominent, as in the Amaltheidæ. Its length in all groups, together with its position, was, however, sufficient to show that the shell must have been carried while crawling more elevated above the arms than in Nautiloids, and therefore in a position bringing greater strain upon the parts of the mantle most used in balancing this organ.

Waagen 2 with his usual keenness has observed, that the annular muscle could not have served solely for holding the Nautilus within the shell, but must

<sup>&</sup>lt;sup>1</sup> Henslow in his interesting book, "The Origin of Floral Structures," (Appleton's Intern. Sci. Series, 1888, p. 88) takes somewhat similar ground, and says that "the forms and structures of flowers are the direct outcome of the responsive power of protoplasm to external stimuli." Also pp. 123, 147, 333–337. See also quotation from Packard's "Cave Faunas of North America," p. 52, note 1, of this memoir.

<sup>&</sup>lt;sup>2</sup> Ansatz d. Haftsmusk. b. Naut. u. d. Amm., Paleontogr., XVII. p. 190.

have been also useful as an air-tight band around the animal, fastening the mantle closely to the shell. The very slight impression made in the inner surface of the living chamber shows that this muscle was not very strong, nor very useful for purposes of prehension, and we are disposed to agree with Dr. Waagen's remark, and even perhaps go a little further. Finely preserved casts of the living chambers of Ammonoids, from Solenhofen and other places, do not afford traces of this annular band, and it seems to have been of a similar nature, but of not so great importance in this order, as the pallial muscles among the Lamellibranchs. The animal of Nautilus was probably held in its shell almost exclusively by pressure, and this band of muscles perhaps served to secure the posterior parts from being disturbed by the movements of the outer parts of the body while the animal was using its hyponome. The supposed muscular band of Oppelia steraspis, figured by Waagen, 1 runs forward on the sides much nearer to the lateral edges of the aperture than in Nautilus. This fact also indicates that the Ammonitine could not have used the fore parts of the body in the same way as the Nautiloids.

The convexity of the central zone of the septum is certainly a differential among Ammonoids when compared with Nautiloids, but it is in strict correlation with the arising and lengthening of the dorsal, ventral, and lateral lobes, especially the first two, and is therefore concomitant with the increasing complication of the sutures, the closer coiling, and the greater involution of the whorl in this order. We have already given the details sustaining this view in our Genera of Fossil Cephalopods, and need only refer here to the cases of Pinnacites (p. 311), in which the septa are double concaves on account of the ridges formed by the large lateral saddles, and the family of the Primordialidæ (p. 316). "While still in the broad-whorled anarcestian stage, the septa are nautiloidean or concave, but when the deep ventral" and dorsal\* "lobes and large lateral saddles are formed, the septa become ammonitoid or convex along the median line." It becomes, therefore, necessary to look upon this differential character as also attributable directly to the habits of the animal, and due to the efforts of the Ammonoid to respond to the requirements of its surroundings.

The persistent ventral position of the siphon is a constant differential among Ammonoids. Even the nostologic series of the Jura and Cretaceous, which yielded so readily to physical changes, becoming uncoiled and departing in many of their characters from the normal ancestral types, still retained the ventral position of the siphon. Although there was considerable lateral variation in the position of this organ in some species, it remained, so far as known, always external or ventral.

The size of the siphon becomes a matter of considerable importance in this connection, and must be considered as throwing some light on this obscure point in the history of the Cephalopoda. The siphon was a far less important organ among the later than among the earlier Nautiloidea. It was also smaller, as may have been already gathered from what we have said above, in the adult

<sup>1</sup> Oρ. cit., p. 193, pl. xi. fig. 4.

<sup>&</sup>lt;sup>2</sup> These two words should have been inserted, but were accidentally omitted. 
<sup>2</sup> Pages 12-17.

or ephebolic stages of a Nautiloid, than in the young of the same individual. The ancient primitive radicals like Piloceras and Endoceras had huge siphons, and were macrosiphonulate, whereas in all the remaining forms it was quite small or microsiphonulate. The siphon was also far less important and smaller among the Ammonoidea as a whole than among Nautiloidea, since there were no macrosiphonulate forms in this order. It was also, as has been stated above, much larger and more important in the typembryos, and in the earlier næpionic stage among Ammonoids than subsequently in the growth of the same individuals.

This organ was also far less important, and smaller and less perfectly formed, among the Belemnoids than among Ammonoids, and finally among the Sepioids it became reduced to a mere rudiment, being distinguished with difficulty in the internal shell.

We can therefore say, with some confidence, that the siphon became reduced in size and importance during the progressive period of evolution or epacme of each group of the Cephalopoda, and also followed a parallel course during the development of the individual. When one reviews the various positions, decreasing size, and lessening importance of the siphon in the various groups of Cephalopoda, he becomes aware that these characteristics correlate with each other, but they do not seem to be dependent upon any other character. They are, however, correlative with higher specialization. Thus, in Nautilus, the position of the siphon is variable; in Ammonoids, a more highly specialized type, it becomes more invariable, and always ventral in nealogic stages; in Belemnites which remain straight, and in those more or less coiled, like Spirula, the siphon is also constant, but on the ventral side of the shell. It seems, therefore, that fixity of position is not dependent upon close coiling, but is purely a condition of specialization, and is an accompaniment of the decrease in size and importance of the organ. The fixity and preservation of this differential character, one of the most important in distinguishing the Ammonoids, could not have been due to natural selection, since an organ invariably tending to become of less importance in every order could neither have been advantageous, nor have offered a favorable lever for this law to work with.

Specialization has in all cases appeared to us to be due, not to natural selection, but to physical selection, or the production of suitable modifications by the action of forces which changed in a similar way large numbers of the same species, perhaps nearly all the individuals in the same locality or same habitat, within a comparatively limited period of time.<sup>1</sup>

<sup>&</sup>lt;sup>1</sup> See in this connection the interesting researches of Dr. A. S. Packard, in the Memoirs of the National Academy of Sciences (IV., Pt. I., p. 137 et seq.), in which this untiring investigator deduces similar conclusions with regard to the action of physical surroundings upon cave animals. He also repeats after these new and profound studies the assertion made in former publications, that natural selection does not appear to him to be a cause of modification or of the preservation of variations, but the result of the action of other factors.

Dr. Packard's own words are as follows: "Such a phrase as 'natural selection,' we repeat, does not to our mind definitely bring before us the actual working causes of the evolution of these cave organisms, and no one cause can apparently account for the result." The causes are "change in the environment," "disuse of certain organs," "adaptation," "isolation," and "heredity operating to secure for the future the permanence of the newly originated forms as long as the physical conditions remain the same."

<sup>&</sup>quot;Natural selection, perhaps, expresses the total result of the working of these five factors, rather than

We do not intend to dispute entirely the action of natural selection and the influence of the struggle for existence, but simply to deny the applicability of the law to the more important modifications and series of modifications which have occurred in the history of animals, taking the fossil Cephalopoda as a type.

We have in former papers conceded the preservation of differentials to the law of natural selection, rather on account of the apparent logical necessity of thus accounting for the invariability of minute differences, like the ventral position of the siphon, the siphonal collar, the short funnel, the convexity of the septa and ventral lobe of Ammonoids, and the divergence of the type from the common stock of Nautiloids which these characteristics indicated, rather than from any firm conviction derived from analytical study.

We think now that the changes in the surroundings acted upon the plastic organism, inducing it to make efforts to accommodate itself to new conditions. Effort, being a reaction from within upon a common organization, necessarily produced similar series of modifications whenever the surroundings were not changed so completely as to lead the phylum away from the original type on lines of extreme divergence. Thus parallelisms occurred between the differentials of the Nautiloidea and Ammonoidea, they were less apparent in Belemnoids, which are more remote in habitat, and may be said to have been almost wholly absent in Sepioids, which are still more remote in habitat, as pointed out above. It passes without saying that the differentials are in many cases new modifications; and, if our position is true, they are adaptive characters, correlative in the Nautiloids with their mixed habitat as swimmers and crawlers, in the Ammonoids with their habitat as reptant forms, in the Belemnoids with their intermediate habitat as leapers or bottom swimmers, and in the Sepioids with their habitat as surface swimmers. The simple lobes and saddles, keelless abdomens, and abdominal sinuses in the shells of the Nautiloids, the dendritic or deeper lobes and saddles and keels and rostra of the Ammonoids, the straight internal shell with its peculiar structures and the guard of Belemnoids, and also the degenerate broad internal shell or pen of the Sepioids, are plainly of this nature. Effort working alone upon a common organism could, of course, not produce such results. It is evident that it must have been assisted by the continuous action of physical surroundings. The law, therefore, as referred to in the Preface, seems to be, that, in so far as causes and habits are similar, they probably produce representation or morphological equivalence between different series or forms of the same type in the same habitat, and in so far as they are different, they probably produce the differentials which distinguish series and groups from each other.

being an efficient cause in itself, or at least constitutes the last term in a series of causes. Hence Lamarckianism in a modern form, or, as we have termed it, Neolamarckianism, seems to us to be nearer the truth than Darwinism proper or 'natural selection.'"

These words are so nearly our own views, and so valuable to us as confirmations of the theoretical results given in the text of this memoir, that we regret not being able to quote still more largely from this thoroughly scientific and philosophical writer.

<sup>&</sup>lt;sup>1</sup> Page vi. No. 18.

## TT.

## GENEALOGY.

#### GENERAL REMARKS.

THE Arietidæ are divisible into three parts or stocks, the Psiloceran, the Plicatus, and the Levis Stocks. Each of the last two were probably derived from different varieties of the single species *Psil. planorbe*, or its geographical affine in the province of the Mediterranean, *Psil. caliphyllum.* Psiloceras can consequently be appropriately designated as the Radical Stock of the Arietidæ, and, as stated above, this genus is also a surviving member of the radical stock of the whole order of the Ammonoidea. It may also be considered as the first branch of the Arietidæ.

The Plicatus Stock has four genera or series, Wæhneroceras, Schlotheimia, Caloceras, and Vermiceras. The first and second depart widely from the normal Arietidæ, and they can be considered together, as if forming a second distinct branch. Caloceras and Vermiceras, especially the latter, are distinctly arietian in aspect, and may be classed together in another or third branch of the family tree.

The Levis Stock has five genera or series, Arnioceras, Coroniceras, Agassiceras, Asteroceras, and Oxynoticeras. The first two are derivatives of the same radical species, and can be closely associated as a fourth branch of the family. Agassiceras and Asteroceras cannot be so closely associated with Oxynoticeras, on account of the wider divergence of the adult characters of the last genus, but they are apparently derivatives of the same radical species, and can therefore be joined, forming a fifth branch. Oxynoticeras thus becomes separated from the rest of the Arietidæ as a sixth branch composed of one genus.

The Plicatus Stock can be followed from Psiloceras into a series of forms having transitional characters, Wæhneroceras, and ending in the production of the peculiar series Schlotheimia, having characteristics widely divergent from those of the normal forms of the Arietidæ in their pilæ, and in their single-channelled keeless abdomens. The sutures retained the peculiar phylliform or psiloceran character. In another direction, the same stock built up in part the normal Arietidæ, producing by gradual modification the vermiceran series. Caloceras, though truly arietian in aspect, was nevertheless much like Psiloceras, especially in its sutures. The latter lost their complicated psiloceran characters in Vermiceras, and became simpler in outline, or typically arietian.

The Levis Stock had no such complete transitions to Psiloceras, and began its modifications at a later time in the Lower Lias, springing at once into the true

<sup>&</sup>lt;sup>1</sup> See Summary Plates xi. to xiv., which should be studied in connection with these "General Remarks."

arietian type in the form and sutures of Arnioceras, and from this the typical genus of the family, Coroniceras, was evolved. The keel, double-channelled abdomen, straight geniculated pilæ, and less complicated sutures of both genera, are similar to those of Vermiceras in the Plicatus Stock.

This normal type was rapidly departed from in the next branch, in which the highly aberrant compressed Ast. Collenoli appeared. This aberrant tendency was still more decidedly brought out in the more rapid production of similar, but more compressed and involute, forms in Oxynoticeras. In this, also, the highest specialization was reached by the introduction of a new structure, the hollow keel, as a nealogic and ephebolic characteristic.

The smooth variety of *Psil. planorbe*, and its immediate congener, *Psil. caliphyllum*, were of course the most primitive forms which occurred in the Lias, and we can treat the whole of the two stocks as a connected group arising in Central Europe from the smooth variety of *planorbe*, though, as a matter of fact, this is probably artificial. The actual process of the evolution of the second branch, and probably of Caloceras, as will be explained in Chapter III., took place in the basin of the Northeastern Alps, and the forms found in Central Europe were migrants. When arranged naturally the genera appear as in the Summary Plates, as an assemblage of distinct and more or less divergent series.

We have considered each separate genetic series as a genus, because it was necessary to do this, or else use a cumbersome trinomial or quadrinomial descriptive nomenclature. Even with the aid of binomials, we have not been able to speak of any series under one name as a single species. Had this rule been adopted, i. e. to treat each series as a single species, the opinions of paleontologists are not now in its favor, and probably no one would have followed us in practice, however much disposed theoretically to praise our conservatism. Even Quenstedt in his most recent work has proposed names for the different groups of Arietidæ all ending in "ceras." They are highly appropriate euphonically, but for the most part are open violations of the law of priority in nomenclature and not systematic in arrangement, though supported by observations and a wealth of accurate illustrations which are of the highest importance to all students of this branch of science.

We have tried to show, in the Introduction and in other parts of this essay, that the metamorphoses of a normal individual in all its stages is a trustworthy index of the morphogenesis of its group, and that a group of species tended to have a cycle of forms corresponding to these metamorphoses. The unit of classification is, therefore, not the species, but the genus; in other words, it is the smallest natural group which is genetically connected, and in which a more or less complete cycle of forms or species may be traced. The genus may also be further defined as an independent group of species, which must always be represented by a distinct diverging line when represented graphically in a geological diagram or genealogical table. In such examples the genus becomes a series of forms, having a distinct line of modifications traceable to the adult radicals, and more or less present in the nealogic stages of their descendants. It has differential characters, but these may be, as in the case of Coroniceras with relation to Vermiceras,

much obscured by morphological equivalents, and in such series the closest study of the structural gradations becomes the only sure guide.

As a rule, a series also runs through a gamut from the discoidal forms to the involute, but not always, because there are series like Caloceras having no involute forms, and no one species of Vermiceras or Arnioceras is more involute than another. Nevertheless there is a decided development of the quadragonal whorl in Vermiceras, which, as shown in the series of species in Coroniceras and Asteroceras, and during the development of the individual in all normal forms of the Arietidæ, is usually an intermediate stage to the future genesis of compressed and involute shells.

In such a system, also, certain radical forms which do not show the usual morphogenetic cycle may occur, as was the case with Psiloceras before the more involute forms of that genus¹ were discovered in the Mediterranean province. These may have a closely allied and inseparable series of varieties,² which cannot be distributed into the different genera arising from them. In such cases, the radical may be considered as an undeveloped series, and separated as a distinct genus, though it consist of but one species with well marked varieties.

A species is a definite step, or gradation in the morphogenetic cycle of the genus, and is distinguished by its form, amount of involution, sutural and other adult and senile characters, and the more or less accelerated development of the nealogic stages. In the descriptions, it will be noticed that the ephebolic characters of the ancestral form, though it may be a closely allied species, are nevertheless often accelerated in the nealogic stages, and the ephebolic stages then acquire some peculiar distinctive differentials. The aberrant pathological forms, and dwarfs of the same species, may often have more accelerated development than the normal forms, and sometimes simulate distinct species. These, as well as the normal varieties of species, have connections with other species which can only be properly estimated with sufficient materials and accurate study. After having secured the genealogy of a series, the species can be determined and separated, but until this is done, the work does not rest upon a secure basis. The possession of a keel, or channels, or a line of tubercles, or increased involution in the adult whorls, may distinguish one species from another in the same series; but the same differences may make the shell appear to be identical with a species occurring in another genus, and thus confuse the classification unless the genesis of the characteristics has been traced.

The order adopted for illustrating the series in the Summary Plates is the result of following out genetic lines, and therefore presents forms in their approximately natural relations, though necessarily having no reference to chronology. The species are connected by lines indicating their natural affinities, and show the relations of the series; but the title, Summary Plates, fully explains the necessarily abbreviated and more or less artificial nature of the arrangement. Comparison with Genealogical Table V. will serve to correct any erroneous impressions which might arise from the study of these plates, in so far as the species of Western Europe are concerned. Those from other localities, also figured in the Summary Plates, will be found by reference to the descriptions.

<sup>&</sup>lt;sup>1</sup> Summ. Pl. xi. fig. 11-13.

<sup>&</sup>lt;sup>2</sup> Summ. Pl. xi. fig. 1, 2; Pl. xii. fig. 1.

## RADICAL STOCK.

Psiloceras caliphyllum, as supposed by Neumayr, may have been the radical discoidal and smooth form from which Psil. planorbe originated. It is a very close ally of this species, differing only in the sutures, and these, like those of other members of the genus in the Northeastern Alps, are phylliform, and have, as we have said, a triassic aspect. Although we are disposed to share Neumayr's opinion that Psil. caliphyllum is the radical of all the Arietidæ, we think, nevertheless, that the evidence of the forms and sutures favors the theory that the Levis Stock of the Central European province all sprang from Psil. planorbe. The sutures of the normal Arietidæ of Central Europe have less complicated margins than those of Psiloceras and Caloceras of the same province; but these in turn are as a rule less complex than those of the same genera in the Northeastern Alps. The Arietidæ, therefore, can be characterized as having degenerated in respect to the sutural margins of the septa. The degeneration of the sutures in Psiloceras planorbe and in Cat. laqueum and Verm. spiratissimum enables one to see that this tendency was general even in the Plicatus Stock; and it is probable 1 that the Plicatus Stock, with the exception of Vermiceras, all originated in the Northeastern Alps from Psil. caliphyllum.

The degeneration of the sutures is due to an arrest of development followed by the retention of nealogic characters, and is purely degenerative. This is, however, accompanied by the evolution of a new character, an increase in the depth and narrowness of the abdominal lobe, in the typical Arietidæ.

### PLICATUS STOCK.

## Wæhneroceran Series.

The interesting forms discovered in the Mediterranean province, and described by Wähner in his "Unterer Lias," show that the closest affiliation existed between Psiloceras and the schlotheimian group. The genus Wæhneroceras, described farther on, contains species like Wæhn. extracostatum, curviornatum, Panzneri, etc., which are transitional between Schlotheimia and the true plicated species of Psiloceras.

## Schlotheimian Series.

In this series the number of forms having the pilæ crossing the abdomen with a peculiar forward bend, especially in *Schlot. catenata*, enable the observer to see that a direct connection by transitional forms must have occurred between this and Wæhneroceras. The similarities are, however, not so close as to be traceable in a series of connecting forms, and one is still left in doubt whether the evolution of this series took place in an earlier formation than that of the Planorbis bed, or in that bed itself. Suspecting that the nealogic stages of *Schlot*.

<sup>&</sup>lt;sup>1</sup> See Chapter IV.

<sup>8</sup> Summ. Pl. xi. fig. 7-10.

<sup>&</sup>lt;sup>2</sup> Mojsis. et Neum., Beitr., II., 1882.

<sup>4</sup> Summ. Pl. xi. fig. 3-6.

catenata in varieties having the most discoidal forms and the pilæ crossing the abdomen without a channel would throw some light on this problem, we begged Professor Emerson to give us some specimens of this species from the Markoldendorf basin for examination. After making several preparations of those kindly sent in reply to this request, the inner whorls and all stages up to the adult were studied. The young to the diameter of 6-8 mm. resemble closely the older nealogic stages of Wwhn. curviornalum 1 and circacostatum, as figured by Wähner.2 The pile are slightly bent forward on the abdomen, are fold-like, as in Psiloceras, and without the sharp bend and tongue-like forward projection which are the primitive indications of a tendency to form a median ventral channel. This tongue-like projection is formed in the next stage, and the pile, which have in the mean time become very sharply defined and prominent on the sides and abdomen, also exhibit a slight flattening or decided depression, in most forms, along the median line of the abdomen. It is evident from these facts that Wähner was right in considering the species of the wæhneroceran series as transitions to Schlotheimia.

#### Caloceran Series.

This series is divisible into two subseries.

First Subscries.—The direct connection of the plicated variety of Psil. planorbe with Caloceras Johnstoni (torus, D'Orb.) has long been insisted upon by Quenstedt, and in his collection the intermediate types are found. There is (1) a plicatus with whorls slightly narrower dorso-abdominally than is usual in this variety, and somewhat more prominent folds; then (2) one with the same form, but still narrower dorso-abdominally, and for this reason with a blunter and rounder abdomen; then (3) a young one of this form precisely similar to the Johnstoni. These show that Johnstoni is an offspring of the plicated planorbis, in which the more gibbous sides, narrower whorls, and rounder, broader abdomens of the young of that form are retained throughout life.

From Johnstoni one can pass by gradations into Caloceras tortile.<sup>4</sup> First, the typical tortile, with young until a late stage, having rounded abdomens and the aspect of the narrower and smoother forms of Johnstoni. These become angular on the abdomen at various ages, without producing a true keel. Secondly, those which introduce a slight keel upon the elevated abdomen, but which subsequently disappears in the increasing angularity of the abdomen in the senile stages. Thirdly, those which introduce a keel, then a squared or quadragonal form of whorl, like that of Caloceras laqueum. Fourthly, those which are of very large size, similar in all their stages, except in the angular abdomen, to the stouter forms of Johnstoni, and like these becoming rounded in extreme old age.

The first variety grades into Cal. Liasicum, which has rounded, gibbous whorls in the young. This has a keel only at a very late stage, or may not

<sup>&</sup>lt;sup>1</sup> Summ. Pl. xi. fig. 7.

<sup>&</sup>lt;sup>2</sup> Unt. Lias, Mojsis. et Neum., Beitr., XII., Pl. xv., xvi.

<sup>&</sup>lt;sup>3</sup> The larger one (2) was fortunately a broken specimen, and showed precisely the same form as (3) in the young.

<sup>4</sup> Summ. Pl. xi. fig. 14; Pl. i. fig. 12-14.

have any, though, as in the keelless tortilis form, the abdomen may become elevated, or very slightly subangular. Wright's figure <sup>1</sup> admirably illustrates such an individual. The Sironotus variety figured by D'Orbigny has a more compressed form and an earlier development of the keel.

Second Subseries. — Caloceras laqueum has many varieties. First, those which develop the keel at a very late period of the growth, and grade into the third variety of Cal. tortile. With these we find, as sub-varieties, some which, either immediately before or at the time when the keel is developed, change by growth the general form of the whorl. The abdomen may become elevated, as in the first senile stage of some varieties of tortile, or depressed, assuming the aspect of carusense or spiratissimum. Secondly, those which develop a keel at a comparatively early stage, and either retain the rounded sides, or become subquadragonal and approximate in form and pilæ to Ver. spiratissimum.<sup>2</sup>

The senile whorl had metamorphoses, which produced an elevated or narrow abdomen, similar to that of *Cal. tortile* at the same stage, though in some varieties the sides were flatter, and there is a nearer approximation to the true trigonal outlines of the old of Vermiceras.

The young of carusense 3 repeated the characteristics of the intermediate forms, but generally produced the keel at earlier periods. These are also lowest in geological position, and pass into other varieties, occurring later geologically, which are of much larger size. In all these larger specimens 4 the form is noticeably subquadragonal in the adult, and also has a keel, and sometimes faint channels. There is a tendency in old age to produce a rounded whorl, with an elevated angular abdomen in the clinologic stage, resembling the same part in the old age of the prominently keeled varieties of tortile and nodotianum. In the large variety of carusense we also find some forms which in their clinologic stage have flattened and convergent sides, with a keel and slight channels. In other words, there are some specimens which show a tendency in old age to change the subquadragonal form of the adult, very much as in the genus Vermiceras. In this species, also, the sutures were observed in one case of extreme age to lose the differentiated proportions of the adult, and partially retrograde, becoming similar to those of Psiloceras.<sup>5</sup> The young and the adult of many specimens of the raricostatum variety of carusense 6 are inseparable from the same stages in the extreme of variety a of raricostatum, with the exception perhaps of slight differences in the marginal digitations.

The typical raricostatum, however, is not similar to Cal. Liasicum, being extremely broad transversely, and having a very immature gibbous whorl, which can be called subquadragonal only in variety b. In old age, even the broad whorl of the typical variety diminished in transverse diameter, the abdomen became more elevated, and the keel and pilæ obsolescent, until finally a fragment of the old whorl cannot be distinguished from the same stage of Cal. tortile or nodotianum.

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    Lias Amm., Pal. Soc., I. p. 316, pl. xvi.
    Summ. Pl. xi. fig. 22.
    Summ. Pl. xi. fig. 1-3.
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Fl. ii. fig. 3, 3 a.
 Pl. i. fig. 16.
 Pl. vi. fig. 15.
 Pl. i. fig. 25 a.
 Pl. i. fig. 24, 25.

<sup>10</sup> Compare section of old nodotianum, pl. i. fig. 10, with section of old raricostatum, fig. 25.

Cal. nodolianum, as found at Semur, has two varieties. One of these resembles the subquadragonal varieties of Cal. carusense until a late stage of development with somewhat flattened sides, similar pilæ, keel, and faint channels. Afterwards it assumed the more acute form of whorl characteristic of its own species. Cal. sulcatum<sup>2</sup> is transitional to Cal. Defineri in its characters, but is not very closely allied. The sutures of Defineri and its young form as seen from the side appear to justify the position given it as the extreme form of the caloceran series. In the Mediterranean province Cal. Johnstoni also occurs, and exhibits transitional characters similar to those of the same species in Central Europe. The pilæ are coarse, like those of the young in Psiloceras, and there is the same tendency to an elevation of the abdomen, as in the same species in Central Europe. Our remarks upon the subseries of this genus in the Northeastern Alps are open to the objection that they were made upon the drawings of Neumayr and Wähner, but our inferences do not differ widely from those of either of these writers, except in the names given to the genera and in the rejection of the name Arietites. We shall sufficiently discuss the details of the subseries occurring in the Northeastern Alps under the heading "Caloceras," in the chapter on "Descriptions of Genera and Species," and shall find that these in part exist also in Western Europe.

The first subseries in the Northeastern Alps contains the well known Cal. Johnstoni. This seems to be the immediate radical of a small series, consisting of Cal. hadroptychum, an unnamed form also figured by Wähner, and the giant Cal. nigromonatum. The last has a keel, but no channels.

This subseries also includes *Cal. Liasicum*, which is very close to *Cal. Johnstoni*, *Loki*, and *Seebachi*, species having very immature keels, shallow channels, and slightly depressed abdomens connecting *Liasicum* with *Cal. Haueri* of the next subseries.

The second subseries includes forms like Cal. proaries, which shows in its development how closely they are all connected with Psiloceras and the forms of the first subseries. This is the representative of Cal. nodotianum of Central Europe, and a close ally of this species, though the young are apparently more immature at the same age in the development of the keel and form of whorl. Cal. gonioptychum appears to connect this with the extraordinary series of Cal. cycloides, Doetzkirchneri, Castagnolai, and abnormilobatum. This is peculiar to the Mediterranean province, and shows that, like Psiloceras in the same region, Caloceras probably had a complete cycle of forms, varying from the discoidal psiloceratitic transitions with more or less elevated abdomens resembling Cal. Johnstoni and tortile to Cal. abnormilobatum, having complicated sutures, more involute, compressed whorls, and a narrowed umbilicus. This series, however, though it evolved an elevated acute keel in the two highest species, did not have deep channels in any species.

This subseries also contains Cal. luqueum, var. scylla, and Cal. prespiratissimum, two forms that approximate to Vermiceras in their characteristics.

The third subseries arose apparently from Cal. Loki or Seebachi. The young

<sup>&</sup>lt;sup>1</sup> Summ. Pl. xi. fig. 16.

<sup>&</sup>lt;sup>2</sup> Summ. Pl. xi. fig. 20, 21.

of its first member, Cal. Haueri, appears to indicate such a line of descent, though of course this can only be considered a suggestion derived from Wähner's figures. Cal. perspiratus and supraspiratus are more or less decidedly channelled, and the last inherits well defined keel and channels at an earlier stage than in Cal. Coregonesse. Cal. ophioides is a very curious species, with an early development of the keel and channels in some varieties, and a very late appearance of these in other varieties, as shown by Wähner. This subseries appears in Central Europe in a few keeled and channelled forms.<sup>1</sup>

The third subseries includes also Cal. laticarinatum, a varietal modification of Cal. proaries according to Wähner, and this leads into several shells with much depressed and very stout whorls, such as Cal. salinarium, centauroides, and Grunowi. We consider laticarinatum as separable from proaries, because of the earlier or accelerated development of the keel, and the broad and depressed abdomen.

There is also a subseries including only the curious *Cal. Sebanum* described by Neumayr, which appears to be a form of Caloceras, possibly somewhat similar to the equally remarkable *Cal. laqueoides* of Würtemburg.

This enumeration shows that the species of the Northeastern Alps, if arranged in natural order, would probably form a greater number of subseries in that province than in Central Europe, though for convenience' sake we have here placed them in the same number of subseries.

#### Vermiceran Series.

The young of *Vermiceras spiratissimum*,<sup>2</sup> before the quadragonal form is fully developed, has a stage in which it approximates both in size and characteristics so closely to some varieties of *Cal. laqueum* that separation is not natural. The comparison of Fig. 17 and 18, Plate I., with Fig. 23, Summary Plate XI., shows the tendency of this species to the production of varieties with channels like those of *Conybeari*. The transition from *spiratissimum* to *Conybeari* has been recognized by many paleontologists; in fact it is not possible to separate these species, though the extreme forms of *Conybeari* have much stouter young, and usually develop the channels and keel at a much earlier age.

Ver. Conybeari has the usual broad varieties, with late development of keel and channels, as in Schlænbachi and the like, and also a form which acquires tubercles, the Bonnardi form of D'Orbigny, and loses them again either in the adult or during the first stage of senility. From this form the transition to ophioides, D'Orb., which has the adult Conybeari form at a very early age, and also faint tubercles, is natural and easy.

The old age metamorphoses of *Ver. spiratissimum* and *Conybeari* are quite distinct from those of Caloceras. The sides showed an increasing tendency to converge, the abdomen became narrower, the pilæ obsolescent, and the geniculæ disappeared. In very large specimens this tendency finally obliterated all traces

<sup>&</sup>lt;sup>1</sup> Summ. Pl. xi. fig. 14-16.

<sup>&</sup>lt;sup>8</sup> Pl. i. fig. 2 I; Summ. Pl. xi. fig. 25.

<sup>&</sup>lt;sup>2</sup> Pl. i. fig. 17; Summ. Pl. xi. fig. 23.

of the pilæ and of the channels, but often left the keel more prominent. The whorl acquired the true flat-sided trigonal form, but never became rounded, so far as yet observed.

#### LEVIS STOCK.

#### Arnioceran Series.

This series begins, when zoölogically considered, with Arn. miserabile, a form very commonly in collections named Amm. plunorbis or psilonotus, on account of its close external resemblance to that species. It has, however, distinct sutures, and acquires by growth a subacute abdomen. During the younger stages, while it is still round on the abdomen, or in varieties with broad abdomens, it is, with the exception of its smaller size, a close reproduction of the adult of Psil. planorbe, var. leve. This grades into Arn. miserabile, var. cuneiforme, which has a more acute abdomen and curved and more perfect pilæ acquired at an earlier age, and from this without a break the series passes into Arn. obtusiforme.

Starting again from variety acutidorsale of miserabile, we can follow another line of affinities. There are some forms of this variety which acquire in the adult a keel with faint but abruptly terminating folds or pilæ, and these lead into a variety of Arn. semicostatum.<sup>5</sup> This species has many varieties, which grade from an immature planorbis-like form <sup>6</sup> to those which are prominently keeled and pilated even at a comparatively early age, <sup>7</sup> and also into varieties which have deep channels on the abdomen.<sup>8</sup> These last are inseparable from Arn. tardecrescens, <sup>9</sup> and when they have numerous pilæ they are inseparable from Arn. ceras. <sup>10</sup> There are also varieties of Arn. semicostatum which fade into Hartmanni, <sup>11</sup> and this in turn grades into the still more compressed Bodleyi. <sup>12</sup> From Arn. Hartmanni, also, we can pass into another compressed form, the true Amn. falcuries of Quenstedt. <sup>13</sup>

Returning again to semicostatum, we find that one of its varieties is distinguished for remarkably raricostatus-like pilæ and a low keel. This when followed out leads to Arn. kridioides. This species in some of its varieties so closely resembles Cal. raricostatum, that for a time it was thought to indicate the direct descent of that species from semicostatum.

There are also some forms, usually identified as Anm. kridion in Germany, which have remarkably broad whorls in the adult, and approximate to the true kridion. These, however, never possess the tubercles of the true kridion, and also have young which prolong the smooth stage and otherwise resemble the young of the stouter forms of semicostatum.

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<sup>1</sup> Pl. ii. fig. 4, 5; Summ. Pl. xii. fig. 2.
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**Pl. ii. fig. 7.

**Pl. ii. fig. 7.

**Pl. ii. fig. 10; Summ. Pl. xii. fig. 14.

**Pl. ii. fig. 10; Summ. Pl. xii. fig. 14.

**Pl. ii. fig. 10; Summ. Pl. xii. fig. 14.

**Pl. ii. fig. 19; Summ. Pl. xii. fig. 6.

**Pl. ii. fig. 19; Summ. Pl. xii. fig. 6.

**Pl. ii. fig. 20, 20 a.

**Pl. ii. fig. 23; Summ. Pl. xii. fig. 7.

**Pl. ii. fig. 28; Summ. Pl. xii. fig. 8.
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<sup>&</sup>lt;sup>2</sup> The apertures are also similar as figured by Quenstedt, Amm. Schwab. Jura, pl. xiii. fig. 27, by Dumortier.

The only signs of old age observed in any specimens were the disappearance of the geniculæ and pilæ, and increasing flatness and convergence of the sides.

### Coroniceran Series.

This series is composed of three subseries.

First Subseries.—The radical form is Cor. kridion, and this species shows direct connection in many varieties with Arn. semicostatum. The similarities of form and characteristics of the young of some varieties in both species indicate mutual affinities, though the young of other forms of kridion have a very different aspect. Three specimens of Cor. kridion from Möhringen in the Museum of Stuttgardt, named from their arnioceras-like forms Amm. Bodlepi, have the precise characteristics of an immature kridion, viz. divergent sides, an elevated abdomen and keel, and tuberculated pilæ. These grade into the typical Cor. kridion, having in the extremely young stages whorls with gibbous, divergent sides, smooth at first, but becoming more quickly pilated and tuberculated.

From these forms the transitions are complete to *Cor. coronaries*, which indeed might be very properly considered as a variety of the same species, since it merely exaggerates all the characteristics of *kridion*. From this we can pass into the true *Cor. rotiforme*,<sup>3</sup> in which the adults differ greatly from *kridion*. The young <sup>4</sup> belong to the typical variety, and are broader and flatter on the abdomen than in *kridion*, and also have divergent sides and very heavy coarse tubercles. Senility is shown only in specimens of exceedingly large size by the very gradual obsolescence of the tubercles, pilæ, and channels, though we have not found any specimens, which had become entirely smooth, or in which the channels had entirely disappeared.

The transition from Cor. rotiforme to Cor. lyra<sup>5</sup> is accomplished through a variety, which is separable from the former only by a single character of no special value. The superior lateral saddle is somewhat pointed and narrow, instead of being cut into on the border by numerous marginal lobes, as in rotiforme. The varieties of lyra<sup>6</sup> which follow have, at an early age, a form similar to that of the adult rotiforme with a more or less elevated abdomen, slightly convergent sides, and tuberculated pilæ. There is also a tendency to increase the abdomino-dorsal diameter of the whorls, the pilæ becoming more closely set and less prominent than in the first described variety.<sup>7</sup> Senility<sup>8</sup> is indicated by obsolescence of the tubercles and the decreasing width of the abdomen. No specimens were observed in which the pilæ had disappeared, though in one specimen they were reduced to broad curved folds, and the channels were almost obsolete, the keel also having been reduced to a low broad ridge. This specimen measured 440 mm., while one at Semur measuring 525 mm. had lost only the tubercles, and the first senile or clinologic stage had but just been entered upon.

<sup>&</sup>lt;sup>1</sup> If Arn. kridioides had been found on the same level with the earliest form of Cor. kridion, it would undoubtedly have to be considered a transitional form between semicostatum and that species; but since it is not found there, perhaps the safest way is to indicate the descent from semicostatum alone.

<sup>&</sup>lt;sup>2</sup> Pl. iii. fig. 3; Summ. Pl. xii. fig. 9.

<sup>8</sup> Pl. iii. fig. 14-17.

<sup>&</sup>lt;sup>4</sup> Pl. iii. fig. 4-9 a.

<sup>&</sup>lt;sup>5</sup> Summ. Pl. xii. fig. 13.

<sup>&</sup>lt;sup>6</sup> Pl. iv. fig. 9-14.

<sup>&</sup>lt;sup>7</sup> Pl. iv. fig. 5, 6.

<sup>&</sup>lt;sup>8</sup> Pl. iv. fig. 15, 16.

From this species we may follow two lines of evolution, one into *Cor. trigonatum*, and one into *Cor. Gmuendense*. The former, *trigonatum*, can be distinguished by its young whorls, which were stouter than is usual in the young of *lyra*, by the increasing amount of the involution, which is no longer confined to the abdominal region, but covers in the geniculæ in some specimens, and by the earlier period at which the pilæ become fold-like and the abdomen subangular.

Cor. Gnuendense is also distinguishable from lyra and from trigonatum by its extremely flattened whorls in the young and adult, though it may otherwise exactly resemble the young of the typical variety of lyra. The involution did not increase by growth, but was confined to the abdominal area, and limited laterally by the geniculæ. The senile changes were very distinct, and occurred at earlier stages than in lyra; the abdomen became narrower and the sides convergent before the loss of the tubercles. Thus we can say with certainty, that, in this species, degradational old age changes began to alter the form before the other adult characteristics showed signs of obsolescence.

The Second Subseries of Coroniceras begins again with Cor. kridion. The connection is made by a very remarkable form, Cor. Sauzeanum. The young in some specimens are like the young of kridion, and then in the next older but still immature stages 4 acquire the characteristics of the adults of kridion. The typical Sauzeanum maintained until a late period of growth, and probably throughout the ephebolic stages in some specimens, the broad abdomen and prominent tuberculated geniculæ of the young, but the sides usually became slightly convergent. Variety Gaudryi, for a greater or a less number of whorls repeated the typical form of Sauzeanum. The geniculæ in older stages were carried inwards, the abdomen became slightly elevated and proportionately narrower, and the tubercles almost obsolescent. A large whorl, over six centimeters in the abdominodorsal diameter, was observed, in which these characteristics were not changed otherwise than by the shallowing of the channels and the depression of the keel.

The transition forms from variety Gaudryi to Cor. bisulcatum<sup>7</sup> are not perfectly satisfactory. They are, however, nearly allied by the peculiarities of the abdomen and geniculæ in the young of bisulcatus, which are similar to those of the young of variety Gaudryi until a late stage of growth. Two specimens of large size were observed. One had a diameter of 620 mm., the tubercles and channels were almost obsolescent, the pilæ very thick and fold-like, but the geniculæ were well developed and prominent, as in the adult. Another, 650 mm. in diameter, had the abdomen much narrower proportionately, the tubercles had disappeared, and the channels were almost obsolete, the keel being much reduced in size. The former was 170 mm. in the abdomino-dorsal diameter of the last whorl, but the latter reached the enormous size of 240 mm. in the same part. There was, therefore, a difference of 70 mm. in the diameter of the last whorl, as compared with the difference of only 30 mm. in the diameter of the entire shell.

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    Pl. vi. fig. 1, 2; Pl. vii. fig. 1; Summ. Pl. xii. fig. 15.
    Pl. v. fig. 4-9; Summ. Pl. xii. fig. 14.
    Pl. vi. fig. 6, 8-9.
    Pl. vi. fig. 9, 10; Summ. Pl. xii. fig. 10.
    Pl. vi. fig. 5, 6, 12, 13.
    Pl. vi. fig. 14.
    Pl. vi. fig. 2-8; Summ. Pl. xii. fig. 11.
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The Third Subscries of Coroniceras begins with Cor. latum.¹ This species is remarkable for retaining, until a late stage of growth, the characteristics of the young of rotiforme, and for its exceptional form, the sides of the whorl being exceedingly divergent, the pilæ fold-like and heavily tuberculated, the abdomen gibbous and slightly elevated.

There is one variety of rotiforme with very stout and gibbous whorls in the young, which cannot be distinguished from one variety of latum until a late stage of growth, except by the singleness of the pilæ. Single pilæ occur, however, in many specimens of all varieties of latum, so that this is not a distinction of constant value. Cor. latum must, therefore, be considered a direct descendant of rotiforme. From this species the transition to Cor. Bucklandi² is accomplished by numerous intermediate forms. These exchanged the form of latum in the young for a sinemuriense-like stage, in which the abdomen became contracted in breadth, the sides parallel, and the channels deep. This stage was retained in some specimens for a long time, while in others it quickly gave place to the huge pilæ, parallel but gibbous sides, transversely broad whorls, and flattened abdomen of the adults of the typical Bucklandi.

In other forms, with similar young, the pilæ assumed during their adult stage the usual aspect, with either only a trace of tubercles, or none. I have not been able to follow the transitions of this, or the sinemuriense variety, into the stout form of Bucklandi. There can be but little doubt, however, that the large form found at Lyme Regis differs only in having had a more accelerated development; i. e. in skipping the double pilæ and large tubercles of the sinemuriense stage. It evidently acquired, at a very early period in the young, large untuberculated pilæ, and in old age was characterized by a very decided narrowing and rounding off of the abdomen, obsolescence and bending forward of the pilæ, disappearance of the channels, and a broader and less elevated keel.

The evidence of transition from the *sinemuriense* variety to *Cor. orbiculatum* rests upon similar grounds. The singleness and perfection of the pilæ are the only differences which separate the young of *orbiculatum* from the young of such forms as variety No. 5 of *sinemuriense*. In the adults, however, the narrowness of the abdomen, flatness of the sides, and their convergence outwardly, are marked differences in aspect, which were greatly increased by advancing age. The abdomen in some very large specimens became almost obtusely angular, as in Vermiceras, and the pilæ fold-like, much bent forwards, and the channels obsolete.

# Agassiceran Series.

This series obliges us to return once more to *Psiloceras planorbe*. It has two subseries.

First Subscries. — The young of Agas. lavigatum <sup>8</sup> had a close resemblance to the young of the compressed varieties of Cor. kridion, and to Cor. rotiforme in some varieties, before the latter acquired tuberculated pile. But this likeness was

<sup>&</sup>lt;sup>1</sup> Pl. iii. fig. 19-23; Summ. Pl. xii. fig. 16.

Pl. iii, fig. 18; Summ. Pl. xii, fig. 17.

<sup>&</sup>lt;sup>8</sup> Pl. viii. fig. 9-14; Summ. Pl. xiii. fig. 1.

due to the stout whorls of the younger stages, and cannot be relied upon as at all conclusive. The stout helmet-shaped whorl is a larval characteristic, derived from the primitive ancestral Goniatitic form, Anarcestes. It is found in all the Ammonitine at an early stage of growth, and may be retained in radical forms until a late stage; and in this species it sensibly influenced the shape of adults. The adults of many specimens of Agas, lavigatum 1 are closely parallel with Psil. planorbe. Dwarfed specimens sometimes have the form and smooth aspect of planorbe, and even the apertures are similar, and Agas. lavigatum, therefore, must have been a direct descendant of Psil. planorbe.2. In var. d of lavigatum the depressed helmet-shaped whorl is exchanged in course of growth for the compressed helmet-shaped, just as in planorbe. The young,3 unlike the adult of planorbe, have short living chambers,4 and the septa are quite distinct, and in most specimens there is a raised siphonal ridge along the abdomen, though the keel is not well developed, nor are the channels present. The misnaming of varieties of lævigatum as Amm. planorbe is also common in European collections.

The same peculiarities are present also in Agas. striaries.<sup>5</sup> In some varieties of this species there are perhaps still closer approximations to the general form and aspect of the smooth forms of Psil. planorbe.

Agas. Scipionianum 6 has two marked varieties, — one less involute, with spines in the adult, and one more compressed, with smaller spines.8

Agas. nodosaries is apparently a compressed form, very similar to Scipionianum. Agas. Scipionis is a distinct species, having smooth and more involute whorls.9

The Coroniceran proportions and aspect of the sutures in Scipionianum are well marked, and would have led to the association of this species with that genus if there had not also been similar sutures in Ast. obtusum, showing that these proportions are progressive characteristics of independent origin in each series. The completeness of the gradations from the adults of Agas. striaries to the young of this species also forbids this conclusion.

### Asteroceran Series.

This series has two subseries.

First Subscries. — The more advanced varieties of Agas. lavigatum 10 have divergent-sided whorls and fold-like pilæ, and a form 11 similar to the tuberculated young of Ast. obtusum, 12 and still more like the untuberculated young of this species. 13 In the accelerated development of the tuberculated variety of obtusum, 14

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<sup>1</sup> Pl. viii. fig. 9, 12.
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<sup>&</sup>lt;sup>2</sup> Compare the young of the last named, fig. 4, pl. i., with fig. 10, pl. viii.

<sup>&</sup>lt;sup>4</sup> Short living chambers are found in the young of Psil. planorbe, and therefore this characteristic is really a confirmation of the assumed direct descent of Agas, levigatum from that species. Agas, levigatum is an arrested development of Psil. planorbe, in so far as the living chambers and its small size are concerned.

<sup>&</sup>lt;sup>5</sup> Pl. ix. fig. 14, 15; Summ. Pl. xiii. fig. 6.

<sup>6</sup> Pl. x. fig. 11-13; Summ. Pl. xiii. fig. 7.

<sup>&</sup>lt;sup>7</sup> Pl. x. fig. 11, 12.

<sup>&</sup>lt;sup>8</sup> Pl. x. fig. 13, and pl. vii. fig. 15.

<sup>9</sup> Summ. Pl. xiii. fig. 8.

<sup>10</sup> Pl. viii. fig. 11.

<sup>&</sup>lt;sup>11</sup> Pl. viii. fig. 14.

<sup>12</sup> Pl. viii. fig. 8.

<sup>&</sup>lt;sup>13</sup> Embryology of Cephalopods, pl. ii. fig. 11.

<sup>14</sup> Pl. viii. fig. 4.

the divergent-sided whorl is noticeable.<sup>1</sup> This is often replaced by a parallel-sided whorl on the fourth volution, and this in its turn is replaced by the convergent sides of the fifth whorl.<sup>2</sup> The divergent-sided whorl, with its tuberculated pilæ, is skipped in the development of some specimens of obtusum, and it is replaced on the third whorl by the parallel-sided smooth whorl and pilæ of the later stage, instead of on the fourth whorl, as described above.<sup>3</sup>

The broad abdomen and the correlative divergent-sided larval form of Ast. obtusum are retained in the adults of some varieties,4 but even in these the pilæ are smooth and without geniculæ, and the whorls discoidal. Notwithstanding this fact and the enormous size reached by some normal specimens before manifesting old age, there are specimens in the closely allied Ast. stellare and acceleratum which exhibit a remarkable tendency to assume retrogressive characteristics, and to inherit them in their younger stages, while still becoming more involute and holding the keel comparatively unchanged. These characters induced me at first to estimate the whole series as geratologous, but this view cannot be maintained. Most specimens lose the tubercles early, or do not have them at all, the pilæ become mere folds, and bend forward, the keel being low and broad and the channels shallow. There is so close a resemblance between these ephebolic characteristics and the old age stages of the common English form of Bucklandi at Lyme Regis, especially in the stout varieties of obtusum, that collectors frequently call the old of Bucklandi by the name of Amm. obtusus. Upon one occasion I was myself completely deceived by the exposed portion of a whorl, which, when finally cleared of its surrounding matrix, was readily identified as a senile specimen of typical Bucklandi. Nevertheless the characteristics of Ast. obtusum, when compared with the radical Agas. striaries or lavigatum, are not geratologous, but nealogic. They have the same relation to the characteristics of these radical forms that the fold-like pile and immature whorls of Cal. Johnstoni have to those of its immediate radical, Psil. planorbe. Their real value as radical characters is shown also by the fact, that in some full grown specimens of obtusum tubercles appear, and in the ephebolic stages of Ast. Turneri of the next subseries the typical arietian characters appear, namely, deep channels, well defined keel, and quadragonal form. These therefore occur in the same succession as in other series of the Arietidæ, and during the growth of the individual they appear in similar order.

Ast. acceleratum, the second and last of this subseries, occurs rarely, but is found in several collections. It has young until a late period precisely identical with the young of certain varieties of obtusum, and the adults of stellare. This stage, which may last until the individuals are from 76 to 89 mm. in diameter, is immediately followed by a stage in which the involution is increased, the sides are flattened, the abdomen narrowed, and the pilæ obsolescent. In fact, during its adult stage a form and characteristics are produced very similar to the stouter varieties of Brooki, with which it was at first associated.

<sup>1</sup> Pl wiii for f

<sup>&</sup>lt;sup>2</sup> Pl. viii. fig. 8.

<sup>&</sup>lt;sup>3</sup> Pl. viii. fig. 8, does not show the inner whorls accurately enough, and a comparison of the figures is necessary in order to give an accurate idea of the development.

<sup>4</sup> Summ. Pl. xiii. fig. 2, has parallel sides, but belongs to this gibbous whorled variety.

Second Subscries.—Some specimens of Amm. stellare, Sow, have a young stage during which the sides become more or less flattened and parallel. These are intermediate between true obtusum and Turneri. The old of the stout varieties of obtusum, and specimens of Turneri in their first senile stage, have characteristics similar to those of the adults of stellare, and occasion confusion in the identification of fragments. The extreme senile metamorphoses of Turneri, when the whorl became smooth, the channels shallow, the sides convergent, and the abdomen narrow, occurred, as in other species, at variable ages, sometimes in shells only 102 mm. in diameter.

The differences between the adult of Turneri and the adult of the next species, Ast. Brooki,2 are well marked in most specimens, but the stoutest and least involute forms of the latter are very closely allied to the former. The adults of the stouter variety of Brooki retained the channels, the keel remained prominent, the sides remarkably flattened, and the pile in some specimens prominent and like those of Twneri, but the whorls were generally more involute. The young have very close resemblance to the adults of Turneri. The young 3 of Ast. impendens had no very close resemblances to Turneri at any stage. They repeated the adult characteristics of the stouter variety of Brooki during the nealogic stages, and in the adults exaggerated the normal tendency to convergence of the sides, depression of the pile, and narrowing of the abdomen. The adult of this variety approximated quite closely to the senile stage of stellare. The fine series of figures given by Wright in his "Lias Ammonites" shows most completely the transitional forms of impendens, and are referred to below in the description of Brooki. Ast. denotatum is simply a more involute form of impendens.

The next species, Ast. Collenoti,<sup>4</sup> can be traced directly to the preceding form, and, if my translation of the facts is correct, it is the geratologous offspring of impendens or denotatum. The young <sup>5</sup> were similar to the young and adults of impendens, and also more remotely to the adults of stellare, but the next or first ephebolic stage was precisely similar in all respects, except the sutures, to the first senile stages of impendens. In the adults of one variety this stage retained distinct pile, though in other specimens the sides became smooth. The involution of the adult whorl was more considerable than in impendens, and the shell closer in this respect to denotatum.

The extreme variety of *Collenoti* had a similar form and development, but was somewhat sharper on the abdomen, and the pilæ were wholly confined to the nealogic stages, the adult stage being similar in form and characteristics, except in the sutures, to the extreme old age of *impendens*. Thus the characteristics of the transient senile stages of *Ast. obtusum* and other normal species were similar to the permanent characters of the ephebolic and even nealogic stages of degenerate or pathological species like *Ast. acceleratum* and *Ast. Collenoti*.

<sup>&</sup>lt;sup>1</sup> Pl. ix. fig. 2, 3.

<sup>■</sup> Pl. x. fig. 6-9.

<sup>&</sup>lt;sup>5</sup> Pl. ix. fig. 10-11 b.

<sup>&</sup>lt;sup>2</sup> Summ. Pl. xiii. fig. 4.

<sup>4</sup> Pl. x. fig. 10; Summ, Pl. xiii. fig. 5.

## Oxynoticeran Series.

The apparently wide divergence from the usual structure of the Arietidæ presented by the hollow keel led me at first to classify this group as a distinct family. The close affinities with the Arietidæ shown by the young, however, and the intermediate characters exhibited by the agassiceran series render such a classification unnatural and undesirable.

The loss of the keel and flattening of the abdomen in the old has no parallel in the normal forms of the Arietidæ, so far as known.¹ It must be remembered, however, that this modification, together with its correlative decrease in the lateral diameter of the whorl, is a fulfilment of the series of geratologous transformations.

First Subscries. — There are two subscries; one, the oxynotum subscries, with comparatively smooth shells, as in the less involute and stouter varieties of oxymotum, and one, the Greenoughi subseries, which has highly developed folds. Both of these series progress in the amount of involution. The less involute Oxyn. oxynotum, the somewhat more involute Oxyn. Simpson; and the still more involute Oxyn. Lymense of the first subseries are parallel with Oxyn. Greenoughi, Guibali, and Lotharingum of the second subseries. According to most authors, we could legitimately consider that the first three were only varieties of one species, though very few would be willing to join the last three under one specific name. The sutures of the adults of the oxynotum subseries are very close together, reminding one of the approximate sutures in the oldest stages of the individual in other genera. The pointed lobes and broad saddles, the short abdominal lobe and long finger-like marginal lobes and saddles, remind us also of the senile peculiarities of the sutures of Cor. trigonatum. The increase in number of auxiliary lobes and saddles and the general aspect of the sutures are, however, upon the whole additional complications, and therefore progressive characteristics.

Second Subseries. — The gradations are uninterrupted from Greenoughi<sup>3</sup> to Lotharingum. The descriptions of the species show that the principal differences consist in the increasing involution of successive species, and a correlatively smoother and more compressed form of whorl.

The young of oxynotum and Greenoughi resemble closely the young of Agas. striaries. There are, however, no intermediate forms between the latter and these two species which would enable one to verify this relation of the younger stages. Whether Oxyn. oxynotum or Agas. striaries gave rise to Oxyn. Greenoughi cannot be decided at present, owing to this deficiency in the evidence; but that both these forms came from the same common stock, and that this stock was Agas. striaries, seem quite probable.

Oxyn. Guibali, the next species of this subseries, bridges the gap between Greenoughi and Lotharingum. The nealogic characters of Oxyn. Lotharingum also show that this species must have been derived from Guibali. Lotharingum, like Ast. Collenoti and other terminal forms of series which have marked geratologous characters, is the smallest form of its own genetic line.

<sup>&</sup>lt;sup>1</sup> Pl. x. figs. 24 and 31.

<sup>&</sup>lt;sup>2</sup> Summ. Pl. xiii. fig. 11.

<sup>8</sup> Summ. Pl. xiii. fig. 13.

Oxyn. Oppeli<sup>1</sup> is a remarkable form, apparently a direct descendant of Greenoughi, which alone survived in the Middle Lias.

Note. — I have so far found but few specimens of the Arietidæ which could not be identified or properly placed in some genetic series. Two anomalies are in the Museum at Stuttgardt, and both were found in the Angulatus bed. One is somewhat similar to the larger forms of Cal. carusense, and is labelled Anm. bisulcatus. It has a very broad abdomen, the sides of the whorl divergent, the pilæ well developed, geniculæ prominent and straight. The keel is low and angular, and two sulcations on either side stretch to the incurved edges of the abdomen and these edges form two ridges as prominent as the keel itself; the sutures are similar to those of Vermiceras. It may be an extreme form of Caloceras, allied to Cal. Haueri, but is apparently not allied to laticostatus, Quenst.

The other specimen is labelled Anm. nodosaries, Quenst. It resembles Agas. Scipionianum in the pilæ and tubercles, the absence of channels, prominent keel, and helmet-shaped outline of the whorl in section. The superior lateral saddles are narrow and deep, the superior lateral lobes also very narrow, long, bifid, and deeply divided by a terminal marginal saddle. The inferior lateral saddles are deep, and occupy nearly the entire breadth of the sides of the whorls, and have deep, rounded marginal saddles.

In the Museum of Amherst, Mass., there is also an enormous shell, which had reached the large size of 600 mm. Though undoubtedly very old and much compressed, it had not yet suffered the loss of its keel, which is plainly apparent, nor the pilæ, even on the extreme outer whorl. The three outer whorls alone are preserved, the centre having been destroyed. The pilæ are about 20 mm. apart on the outer whorl, and have depressed folds. They are more prominent and about 10 mm. apart on the second inner whorl, and about 5 mm. apart on the innermost whorl. No geniculæ or tubercles were apparent, but the specimen would require cleaning before this could be decisively stated. The pilæ were slightly bent forward, and fold-like, as in Caloceras. On the umbilicus were two fossil shells, said to be Plagiostoma gigantea, and the locality where it was found was Dorsetshire, England. The outer whorl was 110 mm. in the abdomino-dorsal diameter, and the slow increase and evidently large number of whorls in the full grown shell, as well as the rotund form of the sides of the whorls and the slight amount of involution and extremely discoidal aspect, indicated a species of either Caloceras or Vermiceras.

<sup>&</sup>lt;sup>1</sup> Summ. Pl. xiii. fig. 16.

### III.

# GENESIS OF CHARACTERISTICS.

Anagenesis, or the Genesis of Progressive Characteristics.

THE introduction of the peculiar pilæ and single channelled abdomen in Schlotheimia, which occurred in the earlier species, must be regarded as a progressive complication, since it is not only a new characteristic, but it is correlative with constant progress in the amount of involution, and with the advent of species having more compressed, more involute and sub-acute whorls. The wæhneroceran series introduces the observer to Schlotheimia by its intermediate modifications when one begins with the radical stock, Psiloceras.

Undoubtedly the steady increase of involution in successive species of the psiloceran, wæhneroceran, and schlotheimian series is, like the similar phenomena of other series, to be regarded as progressive. This is clearly shown, both by the steady increase of size in individuals throughout each series, and also by the fact that these changes are in accord with the general progression of the whole group.

The younger stages, as we have remarked above, were closer coiled during the Mesozoic than in the Paleozoic, and the adult forms were more involute as a rule in the Trias and Jura, than in the earlier geologic periods. The genesis of this progressive character independently in each series may be seen by examining the different series in the four summary plates, and we need not allude to it again in this chapter. It is also interesting to note, that the most exact parallelisms in this respect are to be found between the series, which are widely separated. Thus the extreme aberrant forms of the family, namely, Schlotheimia, Wæhneroceras, the radical Psiloceras, and the opposite extremes of the group, Asteroceras and Oxynoticeras, all possessed highly involute compressed whorls.

Neither of the first three had any species with quadragonal whorls; the shells are all modifications of the helmet-shaped or secondary radical form. There is an approximation to the subquadragonal in the most discoidal species, Schlot. catenata and some others, but this is not very noticeable, and the absence of geniculæ in the pilæ confirm this conclusion. These series, therefore, can be placed in strong contrast with the more normal species of the caloceran series, in which the quadragonal form of whorl and its correlated characters played a prominent part. The acmic species of the progressive series of the Arietidæ were these pilated and tuberculated quadragonal whorls. In the development of the individual, also, the quadragonal form and tubercles are the last characters added by progressive growth, and were primarily of ephebolic origin.

1 'Aνά, upwards; Γένεσις, descent by birth.

Cal. Johnstoni was at first smooth, then ribbed, and the ribs had a peculiar fold-like character, and they appeared in this succession in the young of all the remaining series. The keel was added to these in the adult of Cal. tortile after the pilæ were developed. The adult of Cal. laqueum had the keel, and added also faint channels and in one variety the tubercles. If we are right in referring Cal. Defineri<sup>2</sup> to this series because of its sutures, then the terminal species of Caloceras had a very highly accelerated development, producing the quadragonal form, keel, channels, complete pilæ, and tubercles at nearly the same stage of growth as in Ver. ophioides.

In the development of the young of Ver. Conybeari, the succession of characters was similar,—first a smooth whorl, then fold-like psiloceran pilæ, then keel, then channels, then true pilæ, which often became tuberculated. In Ver. ophioides, a tuberculated species with highly accelerated development, it is difficult to determine whether the keel was developed before or after the channels, since they appeared almost simultaneously.

In the varieties of Cal. laqueum, we found the forerunners of all the rounded, quadragonal, keeled, channelled, and tuberculated forms of Vermiceras. The variety which led into Ver. spiratissimum had no tubercles, and could be called quadragonal, though it had only a slight keel and no channels, or at most very faint bands of depression on either side of the keel. In Ver. spiratissimum, these characteristics are fixed within narrower limits of variation, the keel, channels, and quadragonal form were invariably present in adults, but better defined in some than in others, and no variety with tubercles has yet been discovered. In Ver. Conybeari also the characteristics above mentioned were more invariable, but here we found numerous adult individuals with tubercles on the pilæ, and varieties which produced all these advanced characteristics, including the tubercles in some cases, at a very much earlier age than in other species. Lastly, Ver. ophioides is always tuberculated, channelled, and keeled in adults, though, as shown by its young, evidently derived from those individuals of the tuberculated variety of Conybeari which did not produce these same characteristics at so early an age.

In the arnioceran series, the keel appeared in the young before the channels, and also previous to the development of pilæ. This is the case in Arn. miserabile, and in the derivative Arn. semicostatum. This is in strict accord with an independent descent from the smooth Psiloceratites, but not with a supposed derivation from any intermediate caloceran or plicated form of Psiloceras. The pilæ appeared in the growth of an individual of Caloceras before the keel, — a condition due to the fact that the young remained, as previously explained, very similar to a plicated keelless Psiloceras during the earlier stages of development. The channels were first apparent in the adults of certain varieties of Arn. semicostatum, and in some other species of Arnioceras they became of specific value.

<sup>&</sup>lt;sup>1</sup> This progression was much fuller in the species of the Mediterranean province (see Summ. Pl xi. fig. 17-19), showing the correlations of the development of the individual and evolution of forms in the series better than in Central Europe.

<sup>&</sup>lt;sup>5</sup> Summ. Pl. xi. fig. 21.

There is a similar succession in the evolution of the varietal and specific Thus, in Plate II., Fig. 10, 11, and 15 reprecharacteristics of the series. sent the extreme varieties of Arn. semicostatum, the former with immature pilæ without channels, the second with well developed pilæ without channels, and the third with well developed pilæ and distinct channels. The young of Arn. tardecrescens, Fig. 19, shows that the derivation of this species was probably from the unchannelled forms of Arn. semicostatum similar to Fig. 11. same is true of Arn. Bodleyi with reference to Hartmanni, as is shown by comparing the young of the former, Plate II. Fig. 23, with the adult of Hartmanni, Fig. 17, which had very slight channels even in the adult, and this is still more apparent in the involute flattened form of Fig. 24, in which the channels were earlier developed. The close connection of all its characters, both of young and full grown, with its immediate ancestor, forbids us imagining an independent descent from a variety of any other species than Hartmanni, and the evidence is strong that it had no descendants beyond its own species. The channelless variety of Arn. falcaries, Fig. 26, gives similar evidence of its genetic connection with the channelless varieties of Arn. Hartmanni, or if this is doubted, a more direct connection with Arn. semicostatum may be claimed; but certainly there is no evidence for any connection with the channelled varieties of semicostatum or Hartmanni.

The pilæ began with psiloceran-like immature folds, after the keel appeared in the arnioceran varieties of *Cor. kridion*, and before the keel in the more accelerated development of other varieties of the same species. In some forms the pilæ were completed and became tuberculated before the channels appeared. This same confusion with regard to the time of the appearance of characteristics with relation to each other is a peculiarity of highly accelerated species, as before noted in *Ver. ophioides*.

Such observations are of importance, since they enable us to understand that characteristics do not necessarily develop with invariable regularity. The usual order of their succession may be in a measure changed, or even reversed, when acceleration takes effect upon one character more than another. So far we have found this occurred only in species where all the principal characters of the series were undergoing exceptional acceleration.

The common form of the younger stages of all the Ammonitinæ during the goniatitinula stage is shown in the plates.<sup>3</sup> The depressed goniatitic helmet shape was succeeded in Psiloceras by a laterally flattened helmet shape. In Caloceras the same form was succeeded for a very prolonged period, in species with flattened abdomens, like *Cal. carusense*,<sup>4</sup> by a stage in which the abdomen became broader and the sides slightly divergent. In *Arn. ceras*, as in *Cal. carusense*,<sup>5</sup> this often occurred at a much earlier period, replacing entirely the psiloceran helmet

<sup>&</sup>lt;sup>1</sup> By accident these specimens were all of different sizes. Thus they give false impressions. Although fig. 15 is older and larger than the others here figured, my observations were made on specimens of similar size and age.

Pl. iii, fig. 9, 20.

<sup>&</sup>lt;sup>3</sup> Pl. i. fig. 4 a, for *Psil. planorbe*; pl. vi. fig. 7, for *Cor. Sauzeanum*; also in Embryology of Cephalopods.

<sup>&</sup>lt;sup>4</sup> Pl. ii. fig. 1, 2. <sup>5</sup> Pl. i. fig. 15.

shape, — a fact accordant with the more specialized structure and more accelerated development of the species in this genus.

In Arnioceras <sup>1</sup> the goniatitic helmet shape was replaced by a purely psiloceran helmet shape on the third whorl; and this was retained throughout life in Arn. miserabile, <sup>2</sup> but lasted for a more limited period in Arn. semicostatum, <sup>3</sup> and was then followed by a flatter and broader abdomen, the sides becoming slightly divergent, as in Arn. obtusiforme; <sup>4</sup> and this condition was often maintained throughout the adult stage.

The broad abdomen and divergent-sided whorl, which came out in only a few species of Vermiceras and Arnioceras, and was not very strongly marked in them, became in Coroniceras characteristic of the young at an early stage.<sup>5</sup> It is a significant fact favoring our theory, that in the arnioceran-like forms of Cor. kridion it did not replace the more compressed whorls of the arnioceran ancestor until a late stage of growth. In other species of Coroniceras, however, the broad abdomen and divergent-sided whorl replaced the laterally compressed, helmet-shaped whorl inherited from Arnioceras, as in Cor. latum.<sup>6</sup> All the species of Coroniceras did not have this stage. It was in its turn more or less replaced, in some of them, by the acceleration of other characters, as will be shown farther on.

The law of succession in anagenesis, therefore, is, that progressive species in each separate genetic series were the direct descendants of progressive varieties or forms. The facts consequently are in strict accord with the theory of descent with modification, and with the law of heredity, that like tends to reproduce like.

Coroniceras was not derived from Arn. semicostatum directly, but indirectly, through the more highly specialized forms of Arn. kridioides and Cor. kridion. It was not the varieties of Cor. kridion with arnioceran characteristics most completely developed which led into Cor. rotiforme, but those with divergent-sided and highly specialized pilæ, keel, and channels. So in Cor. rotiforme with reference to Cor. latum, and also in this last with reference to Cor. Bucklandi. These are the purely progressive forms; and their connection with ancestral species occurred through progressive varieties.

## Catagenesis,7 or the Genesis of Retrogressive Characters.

Many large specimens of the species noted in the preceding remarks had narrow abdomens, and the sides converged outwardly. Thus, in what is often mistaken for the full grown adult stage of Caloceras an acute helmet shape appeared, as in some varieties of Cal. Johnstoni, tortile, Liasicum, and nodotianum. This was certainly not, as usually stated by paleontologists, due to a retention of the psiloceran form. It took place after the intermediate or progressive stages in which the abdomen had become widened, more or less flattened, and the sides

<sup>&</sup>lt;sup>1</sup> Embry. Ceph., pl. ii. fig. 8, 9.

<sup>&</sup>lt;sup>3</sup> Compare above with semicostatum, pl. ii. fig. 10 and 15.

<sup>&</sup>lt;sup>5</sup> Pl. iii. fig. 22 a; pl. iv. fig. 1; pl. vi. fig. 6.

<sup>7</sup> Kará, downwards; Γένεσις, descent by birth.

<sup>&</sup>lt;sup>2</sup> Pl. ii. fig. 4-7.

<sup>&</sup>lt;sup>4</sup> Pl. ii. fig. 8.

<sup>&</sup>lt;sup>6</sup> Pl. iii. fig. 20.

gibbous; that is, after the quadragonal whorl had appeared in the development of the same individual.

We have also shown that in every series similar changes took place in the geratologous species, and were accompanied by a correlative series of retrogressive pathological changes in the keel, channels, pilæ, tubercles, and sutures. The convergence of the sides is, therefore, a retrogressive character when it occurs after the gibbous or quadragonal whorl has appeared either in the evolution of the series or in the development of the individual. In Psiloceras a slight convergence of the sides of the whorls was present, and was a primitive character of the helmet-shaped whorl, and this occurred also in *Arn. miserabile*, and in the nealogic stages of other forms of the Levis Stock. Such characters in the individuals of radical species occur before the quadragonal whorl is developed, and in connection with primitive radical characteristics and forms which will not be confounded with geratologous characteristics and forms by any close observer, if he have sufficient materials for study.

There is a true senile degeneration in the old age of some forms, which is apparent in the marked convergence of the sides and sub-acute abdomen of the old whorl, even in such discoidal species as the Psil. pleurolissum.2 This, as a degenerative character, was reproduced at an earlier nealogic stage in the involute species, as may be seen by comparing these figures with those of the involute form Psil. mesogenos.3 The same law holds also in Wæhneroceras. In Schlotheimia it becomes apparent when we compare the old age of Schlot. catenala having smooth abdomen and convergent smooth sides, with the sides and abdomen of Schlot. Boucaultiana which are similar in the nealogic and ephebolic stages. Such characters are therefore retrogressive, and indicate decline in so far as the forms of the whorls, the pilæ, and the channels are concerned, notwithstanding the fact that they are often correlated with the progressive character of greater involution, and appear in the nealogic stages of some (geratologous) species. It will be observed that, in Caloceras from the Mediterranean province,4 the compression of the whorl and other degenerative characteristics occurred without a proportionate increase of involution, and that the same phenomena occurred also in Coroniceras.<sup>5</sup>

The convergence of the sides was evidently a geratologous stage in Caloceras and Vermiceras, but in some species of Arnioceras a slight tendency of the sides to become convergent in the adult stage was noticed. In Arn. semicostatum and tardecrescens, it occurred in the adult stage of varieties with well developed keels, channels, and pile, but not so noticeably in the lower varieties of these species with less accelerated development. In Arn. Bodleyi, where it was found in all varieties, it is noticeable at an early stage, and in the still more highly accelerated development of the involute variety it appeared very much earlier than

<sup>&</sup>lt;sup>1</sup> See also p. 59.

<sup>&</sup>lt;sup>2</sup> Wähner., Unter. Lias Mojsis. et Neum., Beitr., III. pl. xxvi. fig. 4 a, b.

<sup>&</sup>lt;sup>3</sup> Wähner., fig. 3, same plate.

<sup>4</sup> Summ. Pl. xi. fig. 17-19.

<sup>5</sup> Summ. Pl. xii. fig. 14, 15.

<sup>&</sup>lt;sup>6</sup> Wähner, in the work quoted, figures several species of this genus in their senile stages.

Pl. ii. fig. 15.
 Pl. ii. fig. 19.
 Pl. ii. fig. 23.
 Pl. ii. fig. 24.

in any other species of this genus. Thus a high degree of specialization in the development of keel, channels, and pile is correlative with decidedly retrogressive changes.

In Coroniceras, the Bucklandi series exhibits very decided changes in both the individuals and the species. The tubercles were first lost during the old age of the individual, the sides became more convergent even in *Bucklandi* itself, the abdomen narrower, the pilæ reduced to folds and bent like those of the adult of *Ast. obtusum*, the channels shallow and finally almost obsolete, and the keel, even though becoming apparently more prominent on account of the convergence of the sides and obsolescence of the channels, was really not so sharp or well defined.

Cor. orbiculatum exaggerates all these old age changes, becoming narrower on the abdomen, with more convergent sides, and this convergency began even in the ephebolic period in some examples. Similar changes occurred very late in the life of individuals in the next subseries. Thus even the convergency of the sides was not found in the adults of Cor. rotiforme in many specimens, and is but slightly developed even in the extreme old age of some of this species, and in its predecessor, Cor. kridion. This characteristic is, however, observable habitually in the adults of Cor. lyra. These lead into Cor. Gnuendense of the same series, which had very convergent sides in the adult, and was often also destitute of tubercles. The last were confined to the earlier stages of this species, and in old age the changes were very marked and rapid. The extreme variety of Cor. trigonatum inherited convergent sides, smooth and half obsolete pilæ, narrow abdomen, shallow channels, and elevated keel, so early that we may say with confidence they all appeared in the ephebolic period.

The old whorls of Cor. Gnuendense and Cor. trigonatum 1 have the sides of the whorls convergent and a decidedly trigonal form. This form is correlated with obsolescing pilæ and a marked though late decrease in the sutures. These lose the characteristic prominence of the second lateral saddle, which is a progressive characteristic in this genus. All the lobes and saddles also become broader and decrease in proportionate length, and finally in extreme age the abdominal lobe is decidedly shortened.<sup>2</sup> In the Museum of Comparative Zoölogy there was also a much smaller specimen,3 in which the same stage of decline had been reached at an earlier age. The law of succession was, therefore, quite different from that which governed the inheritance of progressive forms. The most retrogressive of the bucklandian varieties were those which were most closely connected in every way with Cor. orbiculatum. The genetic connections also between Cor. rotiforme and Cor. lyra were traceable only through those varieties of rotiforme which had the most convergent sides and the most retrogressive pilæ, tubercles, etc. This also holds for the connections between this last and Cor. Gmuendense and Cor. trigonatum.

The law of succession in catagenesis, therefore, is that retrogressive species in each separate genetic series are the direct descendants of retrogressive varieties or forms. The facts consequently are in strict accord with the theory of descent with modification. The law

<sup>&</sup>lt;sup>1</sup> Pl. v. fig. 8, 9; pl. vi. fig. 3; pl. vii. fig. 1. <sup>2</sup> Pl. vii. fig. 1. <sup>3</sup> Pl. vi. fig. 1, 2.

of heredity, that like tends to reproduce like, cannot be assumed with regard to the transmission of senile characters, since these were probably not directly transmitted from one species to another. Nevertheless, the tendency to degeneration must have been inherited, if we can judge by the appearance of retrogressive characters at earlier stages in successive species.

In the three geratologous series, Asteroceras, Agassiceras, and Oxynoticeras, we find the same laws of anagenesis and catagenesis. The psiloceran-like or progressive species were the immediate progenitors or proximate radicals of progressive varieties, species, and genera in the direct line of descent, but when geratologous forms began to appear, and progression changed into retrogression, there was a corresponding change in the radicals. Then the retrogressive forms arose from varieties which were themselves also proportionately degenerate, and had similar retrogressive and geratologous characters.

The progressive stage with divergent sides and broad abdomen, which appeared in the young of Ast. oblusum and was found in some adults, was suppressed, and was replaced by a modified quadragonal form in Ast. Turneri. This in turn was replaced by the tendency to accelerate the development of the trigonal convergent-sided whorl and its correlative retrogressive characters, the untuberculated pile, low broad keel, and shallow channels, in Ast. Brooki, impendens, and denotatum. The geratologous trigonal form appeared at an earlier age in each successive species, until at last in Ast. Collenoti<sup>1</sup> it took possession of the earliest nealogic stages.

The retrogression of form in the series of species may often be compared with parallel pathological series of individuals, which may be made within a single species. Ast. stellare 2 had dwarfed forms, much smaller than most of the healthy adult specimens of its own species. These last, though so much larger, ordinarily showed no signs of old age, while the dwarfs were completely changed by senile metamorphoses. Much smaller but similarly dwarfed specimens occurred in Ast. acceleratum, with even more compressed and prematurely aged whorls.3 A remarkable series of these dwarfs, from which the two figures referred to in the notes were drawn, is to be found in the Museum of Stuttgardt. The smallest of these completely geratologous specimens is not over half the size of the largest, which itself is not of average size, as stated above. The comparison of these dwarfs with the more involute varieties of Ast. Brooki and the adult of Ast. Collenoti shows that they cannot have been connected by direct inheritance. They were evolved independently of these geratologous forms, and I am not calling upon the imagination to fill any blanks when I speak of them as homoplastic morphological equivalents of Ast. impendens and Ast. Collenoti. It can hardly be doubted that the geratologous forms, when found as dwarfed varieties within a species, are the products of the unfavorable action of the surroundings, or, in other words, that they are more or less diseased individuals. Their close parallelism in every respect with Ast. Brooki, impendens, and Collenoti shows that we can attribute with great probability the origin of all such forms to similar pathological causes.

With regard to the agassiceran series, it may be remarked that the quad
1 Pl. ix. fig. 10-11 b; pl. x. fig. 10.

2 Pl. x. fig. 1, 2.

3 Pl. x. fig. 3.

ragonal form, or rather an immature representation of it, occasionally occurred in some adult individuals of Agas. lævigatum, in which the sides were flatter than usual. In Agas. striaries the quadragonal form and the siphonal line or keel were more decidedly expressed, as well as the tendency to elevate the abdomen. In Agas. Scipionianum after the earlier nealogic stages were passed which closely resembled the full grown of striaries, with the exception of the thicker pile and somewhat deeper umbilicus, the adult showed a quadragonal whorl with a keeled abdomen and tuberculated pile. The old age had a smooth trigonal whorl. In Agas. Scipionis, which is a naturally distinct form, the extreme varieties had more involute whorls, smooth pile, and became trigonal and smooth at an early stage.

Thus, at all stages of growth and decline, the correspondence or parallelism between the individual and the morphogeny of the series is complete.

In the second subseries of Oxynoticeras we have found that there was one species, Oxyn. Lotharingum, in which the whorl during the last senile stage became completely rounded on the abdomen. The sides became gibbous and narrower, thus showing a slight tendency to revert to the primitive form of the less discoidal Agas. striaries and Psil. planorbe. These similarities were also greatly increased by the appearance of senile folds similar to the primitive pilations of this species and Psiloceras. The adults of the species of this subseries were also geratologous, in so far as the forms were not only much compressed and trigonal, but also smooth. The degeneration and the total loss of the hollow keel also occurred in this oldest stage. We should not be at all surprised if species should be found, and identified as belonging to this series, in which the hollow keel was either not present at any stage, or was only slightly indicated during the nealogic stages. These adults would then correspond to the geratologous stage of Oxyn. Lotharingum, in the same way that Ast. Collenoti corresponded to the old of the normal forms of Ast. obtusum and stellare.

If a tendency to the inheritance of retrogressive characters be granted, and certainly their occurrence at earlier stages in successive species makes this view seem highly probable, then the same law of replacement which produced progression would now act upon successive organisms so as to produce retrogression. The observed phenomena indicate the direct replacement of the characters of progressive ancestors by degenerate characters, which were first observable in the old age of these ancestors themselves. If there had been in most cases simply a mass of degenerate forms, without any definable evidences of successive gradations, as in the famous instance of the Magnon examples of distorted Planorbidæ, it would be possible to say at once that the parallelisms of the geratologous period, with retrogressive characters in what we have called geratologous species of the same series, were purely homoplastic correspondences. On the contrary, the gradations are perfectly well marked, as we have described them above and in the Introduction to this monograph, and the replacement of progressive characters by the geratologous takes place in strict accordance with the law of acceleration in heredity.

<sup>&</sup>lt;sup>1</sup> Summ. Pl. xiii. fig. 8.

We can make our meaning plainer by comparing this cycle to an imaginary cycle in the history of architecture. The buildings of primitive times would necessarily be substantial, plain, and suitable to the limited wants of the people; then, as wealth increased, the architects would respond with showy structures, having more ornamentation, and more complicated interiors. We will suppose that they had begun to place most of their ornamentation in and upon the central parts of the modern buildings, and, out of deference to inherited canons of taste, had always, even in the most florid acme of their progress, adhered to this law, leaving foundations primitive in style and uppermost portions always unadorned. As time progressed, these structures would assume vast proportions, and would be built in ever increasing numbers, until at last the nation, having outgrown its strength, would begin to decline. The vast buildings would have to be abandoned, and smaller habitations would arise, in answer to the requirements of a poorer population. The architects, faithful to their inherited canons, but forced into simplicity, would gradually follow the decline, and record it in the structures of the decadence. They would effect this, we will suppose, by reducing the ornamentation from above downwards, thus gradually doing away with the central band of ornamentation, and also by actually lessening the height and otherwise contracting the bulk of the buildings. Primitive simplicity would thus be restored, but strong traces would still be left in the style and construction of the buildings of their having been adapted, by a process of reduction, from a previously existing period of greater size and complexity in structure. It would be possible to read in the style of the decadence, that all the buildings had come from primitive forms through the medium of a progressive period, during which the central stories had undergone the greatest modifications. This would be traceable in many surviving peculiarities of the modes of laying the courses of stone, the cutting and more elegant shaping of the interiors, etc. It would, however, be equally plain that the architecture of the upper stories had always been more or less degenerate, and also that their degenerate forms had replaced the progressive ornamentation and forms of the central parts of buildings during the decadence of the nation.

This would quite accurately represent the reversion of the forms we have been tracing, so far as the purely retrogressive series were concerned. We can understand their structural degeneration and their positions as the latest evolved forms of each series upon the same grounds, since they would necessarily stand at the termini of the series. Their degenerate characters could not be said, perhaps, to have been inheritable, any more than the architecture of the buildings alluded to above, but a tendency to degeneration caused by the unfavorable surroundings would have to be assumed. Each generation in succession, acted upon by this tendency, like the successive buildings of the decadence, would arrive earlier at a stage when senile characters would replace the progressive characters of the adult period. The geratologous characters are, however, in greater or less degree, reversions due to the loss of the progressive characters of the adult; and this is equally true when the characters of geratologous species are compared with those of the simple, generalized radical species from which

the group originated. That these reversions are the remnants of the earliest acquired structures and physiological powers seems perfectly plain, in view of the well known case of the return of childish structural peculiarities and memories in man after his adult peculiarities and powers have been exhausted.

The peculiarities of series which, like Oxynoticeras, presented certain highly progressive or novel characters in combination with retrogressive characters, have been sufficiently described in these pages. It only remains to add, that such types are not uncommon in the different families of the Ammonoids and Nautiloids, and therefore they must not be considered as unique.

#### DIFFERENTIAL CHARACTERISTICS.

The differential characteristics have already received a considerable share of attention, but it still remains to review them in each series. The diagnosis of each genus is necessarily deceptive, in so far as it gives false views of the invariability of the differentials.

The psiloceran series presented an altogether peculiar helmet-shaped whorl, with more decided congeners in the Trias than in the Lias. The involution increased in successive species, and in correlation with this tendency the complication of the sutures also became greater.

The marked differentials of Wæhneroceras, which are transitional from the plicated forms of Psiloceras to the series of Schlotheimia, the retention of the psiloceran form and sutures, the geniculess pilæ, and the nascent channel on the abdomen are so obvious, that they need only be mentioned and attention again be drawn to the very remarkable fact, that, as in Psiloceras, this series departed from the discoidal radical, and exhibited increase of involution in successive species.

Starting from *Psil. planorbe*, var. *plicatum*, as the radical discoidal progenitor of the remainder of the Plicatus Stock of the Arietidæ, we find that the compressed helmet-shaped whorl was exchanged in *Cal. Johnstoni* for a more gibbous rounded whorl, but the discoidal character of the shell was maintained, and the pilæ did not have geniculæ or tubercles except in the highest species. There was also a tendency in *Cal. Johnstoni* towards a complication of the margins of the sutures through the deepening of the lobes and saddles, which was especially noticeable in *Cal. nodotianum*. This increase of complication took place especially in the marginal lobes, and there is a backward trend of the auxiliary lobes and saddles, which causes a close likeness between the tendency of the progression in this genus and that of the involute forms of Psiloceras. In Caloceras, however, it

¹ We can mention as similar cases the following: Subclymenia with its ventral lobe and ventral siphon, a true Nautiloid of the Trigonoceratidæ; Pteronautilus among the Gonioceratidæ with its winged aperture; Centroceras among the Hercoceratidæ with a deep V-shaped ventral lobe. Among Ammonoids there are the genera Pinnacites and Celæceras with remarkable sutures among Nautilinidæ; the Gonioclymenidæ with ventral lobes instead of continuous saddles in the Clymeninæ; Beloceras with its extraordinary sutures, and Medlicottia with its remarkable ventral lobe and first pair of saddles among the Prolecanitidæ; and a host of others.

took place independently of increase in the breadth of the whorl by growth, or of increase in the involution of the successive species.

The radical species of the laqueum subseries showed a completely arietian form of whorl. This appears in Cal. laqueum as quadragonal in section, with a keel, faint channels, and straight pilæ, tuberculated in one variety. This form was perpetuated in Cal. carusense of the Upper Bucklandi bed; the keel and ribs were, however, somewhat more highly developed in one variety of Cal. raricostatum. The deep narrow abdominal lobe, also a peculiar arietian characteristic, appeared in Cal. carusense, and was perpetuated in raricostatum; it was reproduced at a very early age in the last species, and in Cal. Defineri. The peculiarities of the straight or curved, fold-like, and crowded pilæ are differentials of importance, which correlate with the other immature transitional characteristics of this series. The series described in the chapter on Descriptions of Genera and Species discovered in the Northeastern Alps shows that highly compressed forms with acute abdomens occurred also in this genus. Cal. Castagnolai had a tendency towards increase of involution, though this shell, and even the extreme form abnormilobatum, must still be classed as discoidal.

In the radical species of Vermiceras, Ver. spiratissimum, the whorl became quadragonal with flattened sides and abdomen, channels, and pilæ with arietian geniculæ. These characteristics were maintained throughout the series, becoming more intense in Ver. Conybeari, and inherited at a very early nealogic stage in Ver. ophioides. The shells remained discoidal, however, as in Caloceras, even in the largest specimens. Looking back, we see that the radical species, Cal. Johnstoni and laqueum, and Ver. spiralissimum, formed a series of proximate radicals, in which there was a regular gradation in the intensity of expression of the different characters after they were once introduced, culminating in the quadragonal form and arietian sutures of spiratissimum. We could, therefore, with perfect propriety associate these three forms in a distinct series, and they would then be related by gradations parallel with those occurring in either Caloceras or Vermiceras, though composed solely of radical species. This is possible because of the discoidal forms of the species of the vermiceran branch of the Plicatus Stock, all of which have numerous whorls, and retain the very long living chambers, at least one volution in length, of the Psiloceran Stock.

The differentials of the Levis Stock had a more abrupt beginning, the transitions from Psil. planorbe to the first form, Arn. miserabile, or the lower varieties of Arn. semicostatum, having been less complete, and the forms separated by a certain interval of time. There was also a much quicker transition from the helmet-shaped whorl to the quadragonal. This took place in the first species of the first series, and this radical, whether the one or the other of the two mentioned, is keeled in adults. In Arn. semicostatum, also, the pilæ assumed in most varieties the peculiar straight, trenchant aspect, and the prominent and square geniculæ, which are characteristic of this genus. In Arn. miserabile and semicostatum the keelless, smooth form of Psil. planorbe, var. leve, was retained so long in the growth of some individuals that it became characteristic of some varieties, and in other species of this series, though less important, it is always found as a

marked characteristic of the umbilicus. The sutures are also peculiar in the simplicity of their marginal outlines and proportions, and these peculiarities remain constant.

In the adult and young of some varieties of the radical species of the coroniceran series, Cor. kridion, a form appeared having strongly divergent sides, lyreshaped tuberculated pilæ, sutures with deep abdominal lobes and prominent inferior lateral saddles, while in the young of other varieties there was a nearer approximation to the young of Arnioceras. In all the succeeding species of the series except Cor. Sauzeanum, a direct descendant of kridion, this divergent-sided, broad-abdomened whorl was found at an early nealogic stage, having the same lyre-shaped pilæ, deep channels, and arietian sutures.

On looking back, we see that Arn. miserabile, semicostatum, kridioides, and Cor. kridion, may be considered as a series in which kridion was a terminal species with an accelerated development in some varieties, and that from this last highly specialized form arose, as we have stated above, the species of the highly progressive coroniceran series, the typical acmic series of the Arietidæ. The arietian differentials, the long abdominal lobe and prominent inferior lateral saddles, and the combination of these with the quadragonal whorl, highly developed keel, channels, and geniculated and tuberculated pilæ, were barely indicated in the caloceran series, and appeared in perfection only in the higher species of Vermiceras. Although they were generated with great rapidity in the arnioceran series, yet they were present in full perfection and were comparatively constant only in the species of the coroniceran series, which, as we have said, were directly derived from Cor. kridion, a species in whose adults these characters first appeared in their final arietian shape and proportions.

The remaining series, which can be properly called the geratologous genera of the Levis Stock, form a distinct group composed of a central series and three lateral series, offshoots from the common radicals, Agas, lævigatum and striaries. The necessary mode of arrangement places Asteroceras on the left, Agassiceras in the centre, and Oxynoticeras on the right. The structural characters also agree with such an arrangement. No progressive linear series can be formed out of the radical species of these series, as in the genera mentioned above the arrangement is necessarily radiatory like the spokes of a fan. The differentials of the adult of the radical species Agas, lævigatum were quite constant in the species; we refer to the discoidal smooth whorls and fold-like pilæ, the simple but arietian sutures with their deep abdominal lobe and prominent inferior lateral saddles. The shell also had fewer whorls and shorter living chambers than the adult of Psiloceras planorbe. In Agas, striaries there is close similarity to lavigatum, but very distinct striæ and a larger size. In Agas. Scipionianum, the prominent keel, channelless abdomen, pilæ, and tubercles were abruptly introduced, and were the principal differential characteristics which distinguished the series from all others in the Arietidæ. This abrupt introduction indicates the former existence of intermediate forms which remain to be discovered.

It may be that a true hollow keel may have appeared in Scipionianum, as is

<sup>1</sup> Summ, Pl. xiii. and xiv.

described by Quenstedt, though we failed in getting positive evidence of anything more than a large solid keel. This, though distinct from the usual arietian structure of this part, had not the black layer above the siphon which distinguishes the typical hollow keel of some species in Oxynoticeras.

In the well known species, Ast. obtusum, the radical of the asteroceran series, the keel was broad and low with shallow channels, and the pilæ were fold-like with either small tubercles or none, and the sutures in adults were like those of Coroniceras. The changes in course of growth from the divergent-sided to the convergent-sided whorl were rapid in some varieties, though in others the broad-abdomened and gibbous-sided whorl was retained even in adults. In Turneri, keel, deep channels, and quadragonal whorls were correlated with peculiarly flattened and broad sides. These species showed a tendency to specialization parallel with those of Coroniceras; nevertheless, in varieties of Turneri, and in the succeeding forms Brooki and Collenoti, the differentials, with the exception of the keel and sutures, tended to become extinct in consequence of the prepotent influence of heredity in the transmission of geratologous characters.

Parallel phenomena were also observed, as stated above, in individuals of preceding series during old age, when the adult differentials disappeared, and also in the adult stages of certain geratologous species of the progressive Coroniceran series, Cor. corbiculatum, Gmuendense, and trigonatum, in which the quadragonal form, tubercles, etc. were similarly affected.

In Oxyn. oxynotum, the differentials which enabled us to separate this from Ast. impendens and Collenoti were the hollow keel and the sutures. The hollow keel appeared, as has been shown, in Oxyn. oxynotum, but it was filled with layers of shell, though in other species it was really hollow, and appeared during the nealogic stages. The increase of involution was correlative with the steadily increasing breadth and flatness of the sides, and an intensified trigonal outline. Oxyn. Lymense 2 was more involute, more acute, and smoother even than oxynotum. The differentials of the Greenoughi subseries were less important characters. They consisted of a stouter form of whorl, which was more like that of  $A_{\xi}as$ . Scipionianum, and fold-like pilæ. These are less pronounced in the higher species, Oxyn. Guibali and Lotharingum, in consequence of the prepotency of the geratologous tendencies shown in the more compressed, more involute, and smoother whorls.

The genera of the Levis Stock had, as a rule, shorter living chambers, usually less than one volution in length, and differed in this respect from the genera of the vermiceran branch of the Plicatus Stock.

The important fact should be noted here, that in all individuals and series the sutures were the last to yield to degeneration, and the characteristics of these are considered by most authors as the pre-eminent differentials of the Arietidæ.

In estimating certain characters as differentials, we mean only those which can be artificially separated and contrasted in different series of the same family, and which may be therefore peculiar to some one series or genus. When a more specialized series is contrasted with an ancestral radical species or series, then

<sup>&</sup>lt;sup>1</sup> Summ. Pl. xiii. fig. 2.

the equivalent or parallel characters are often differentials. Thus, the keel was varietal in the lower species of Caloceras as compared with Psiloceras, and became a differential in the higher forms. The same held good for the quadragonal form of Vermiceras, and its arietian sutures. A very instructive comparison may be made between the cretaceous angulatus-like forms of Hoplites, and their approximately exact morphological equivalents in Schlotheimia, and yet no one well acquainted with their development and genesis would hesitate to use the channelled abdomen, pile, and form in both genera as true differentials. These characteristics do not indicate affinity between these cretaceous forms and Schlotheimia.

Vaeck, in his article upon the hollow keel of the Falciferi, makes somewhat similar statements, and gives details showing the presence or absence of this peculiarity in different species of Harpoceras. Though not prepared to agree that these forms really belong to the same genus, it has been evident to us for some time that the hollowness of the keel was a characteristic which was homoplastic in several distinct series, and it is not a mark of genetic affinity with Oxynoticeras, unless accompanied by other characteristics showing that the descent of the species possessing it was probably traceable to Oxynoticeras. Unless the nealogic stages show traces of this ancestry, it is not in itself a differential characteristic sufficient to bind the forms possessing it into the same genus.

The development of the keel, channels, and pilæ in Arnioceras shows that they were new modifications in this series, as they were also in Caloceras. The keel, after its appearance in varieties of Arn. miserabile, became of specific value in semicostatum, and remained thereafter constant. The straight pilæ and peculiar geniculæ were also first of varietal value in miserabile, and then approached specific importance in semicostatum, and became constant in other species. The channels were variable in all the species in which they appeared, except one of the most highly specialized, Arn. ceras. We have not, however, seen many specimens of this species, and it is not unlikely that this form may, upon further research, prove to be as variable as the more generalized species.

<sup>&</sup>lt;sup>1</sup> Bemerk. u. d. höhlen Kiel d. Falcif., Jarhb. geol. Reichs., XXXVII., 1888, p. 311.

### IV.

#### GEOLOGICAL AND FAUNAL RELATIONS.

## REMARKS.

THE point of view in this chapter naturally rests upon the assumed existence of a persistent series of discoidal shells which formed a continuous radical stock for all the Ammonoidea, beginning in the Silurian and having their last representative in Psiloceras of the Planorbis bed. This, as we have said above, was closely allied to Gymnites of the Trias, and enables us to connect all the Ammonitinæ of the Jura directly with the more ancient primary radicals of the central trunk of the genealogical tree. The chronological distribution of this trunk of forms must be actually represented by more or less broken lines, until all the gaps now existing between the different systems or periods in the earth's history have been filled by the progress of discovery.

The surviving genus of the trunk stock, *Psiloceras*, consists of a series of species which we have called the Radical Stock of the Arietidæ, which became in the Lower Lias the generator of new series of peculiar modifications, spreading out from *Psil. caliphyllum* or *planorbe* like the spokes of a fan, each genetic radius being composed of a separate series of modifications or species. We have given this classification above, and shown that the chronological distribution of the species in each series is in accord with their positions in the series; it now remains to apply the same classification to the solution of the problems of chorological distribution.

There are many more or less complete lists and monographs of local faunas in the province of Central Europe, and extensive collections, which afford a solid basis for comparison. The preliminary work of Prof. Jules Marcou, in synchronizing the minuter subdivisions of the Jura in Central Europe, was completed by the more extensive application of the same principles by Oppel, who visited, studied, and synchronized the faunas of the different localities, and identified the same beds in a large part of this province. The illustrated publications of Hauer, Neumayr, Wähner, Geyer, and Herbich, have also thrown a strong light upon the peculiarities of the faunas of the eastern part of Europe, particularly the basin of the Northeastern Alps. All of these researches, and many others not mentioned, have made still further advances in the classification of the chronological relations of the minuter subdivisions or beds practicable.

- <sup>1</sup> Roches des Jura, pp. 23, 162, 173, et seq.
- <sup>2</sup> Die Jura-Format. Eng. Frankr. u. d. südwestl. Deutschl. Württ. Jahresb., XII. XIV., 1856.
- <sup>3</sup> Die Cephal. a. d. Lias d. nordöstl. Alpen, Denksch. Akad. d. Wissensch., Wien, XI.
- <sup>4</sup> See note 2, page 86. 
  <sup>5</sup> Mojsis, et Neum., Beitr., II. VI.
- <sup>6</sup> Ceph. heirl. Schich, Abh. k. k. geol. Reichsans., XII.
- 7 Das Széklerland, Mitt. Jahrb. d. k. ungar. Anst., V., Pt. II.

The principles of geographic distribution first announced by Marcou<sup>1</sup> have been carried further by Neumayr,<sup>2</sup> who has defined the homozoic bands of life in the faunas of what he has denominated the Mediterranean, Central European, and Russian provinces.

Neumayr, in his article "Ueber climatische Zonen der Jura und Kreidezeit," describes the boundary between the Mediterranean and the Central European provinces. This line, as far as traced by him, begins at the east between the Donetz and the Crimea, at about 47° north latitude, and runs thence to the easterly end of the Carpathians; thence, north-northwest to the neighborhood of Krakau; thence, southwest towards Vienna, and south of Brünn; thence, westerly to the neighborhood of Lake Constance; thence, west-southwest, and later southwest through southeastern France; thence, across the Gulf of Lyons to Spain, and across that country and Portugal to between 38° and 39° north latitude on the Atlantic. This author regards the Mediterranean province south of this line, and the Central European province north of it, as respectively parts of two homozoic bands, which encircled the earth during the jurassic period.

The Central European province was defined by Neumayr, in a general way, as including the British Islands, France, Germany, Bohemia, Moravia, and Poland, north of the line described above, and perhaps the Dobrudscha region. The Jura north of these countries was included in his Russian province, which contained Central Russia, Petschora Land, Spitzbergen, Greenland, and perhaps Vancouver's Island in North America. Neumayr quotes the works of various authors upon the fossils found in South America, and concludes that the Jura in Bolivia, Chili, the Argentine Republic, Columbia, and in Central America is probably Mediterranean. He thinks also that the few fossils found in the United states indicate the presence of a Central European fauna.

Waagen, in his "Fauna of Kutch," shows that India is a distinct basin, containing forms of the Upper Jura found in the provinces of the Mediterranean and Central Europe, besides numerous peculiar species. Steinmann is of the same opinion with regard to the fauna of the Upper Jura which is found near Caracoles in Bolivia.

We have examined a number of the latter collected by Alexander Agassiz at this locality, also several species collected by him at the pass of Tilibichi in Peru, as well as those mentioned in the chapter "Descriptions of Genera and Species" of this work, and have read Gottsche's "Paleontology of the Argentine Republic." These and other sources of information show, we think, the same history as in India; namely, that this region may be advantageously separated as the South American province on account of the number of peculiar species it contains. There are, over and above these, also a number of forms identical with those of Central Europe and the Mediterranean. We have also seen the fossils of the Upper Jura, found in California, through the kindness of Prof. Joseph

<sup>&</sup>lt;sup>1</sup> Roches des Jura, pp. 74-91, 230, et seq.

<sup>&</sup>lt;sup>2</sup> Ueber Juraprov. Verh. k. k. geol. Reichsans., 1871, p. 54; Ueber unverm. auftret. Cephal., Jahrb. geol. Reichsans., XXVIII., 1878; and Jurastud., Ibid., II., 1871, p. 524.

Denksch, Akad. Wien, 1883, XLVII., and also Geog. Verbreit, d. Jurafor., Ibid., L., 1885.

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Leconte, and have collected some forms in California and other localities in the United States. There are also a few species in the collections at San Francisco, but these and the fossils collected at Vancouver's Island, and described by Mr. Whiteaves of the Canadian Survey, which we have also seen at Ottawa, show a mixture of the species of the European province besides a number of peculiar forms. Though not disposed to give any final opinion at present, the facts justify the suggestion that the North American assemblage of species has a distinct facies of its own, and ought to be separated at least provisionally from the South American and all European faunas as the province of North America.

The collections so far made in the Jura show that there is a prevalence of the Arietidæ in the Lower Lias, and of the species of Perisphinctes in the Upper Jura of the South American province, whereas these are less abundant in North America. Whiteaves also shows a mixture of the species of the Cretaceous with those of the Jura at Vancouver's Island, which, together with the peculiar species found there, suggests a distinct basin for that locality as compared with the Jura farther to the south and east in the United States. The fossils so far found in the district of Atacamas, and at localities in the Argentine Republic, show that a provisional separation should be made between this region and that of northern Peru, and that two basins at least, if not more, exist in the Jura of the South American province.

Both the physical features of the distribution of the deposits and the faunas appear, therefore, to make it doubtful whether the terms Mediterranean, Central Europe, and Russia can be assumed as appropriate names for the homozoic bands of the jurassic period in America. It would be preferable to adopt for these bands the nomenclature of Marcou. Thus, the Bande¹ Homozoique Centrale of Marcou would become the Tropical Homozoic Band; the Bande Homozoique Neutrale du Nord of Marcou would become the Temperate Homozoic Band; and the Bande Homozoique Polaire du Nord of Marcou would become the Polar Homozoic Band. These bands could then be subdivided into provinces and basins according to the faunas, and the real facts of the distribution of forms more clearly shown than by using the names of European regions for that purpose.

Waagen, in his article "Ueber die Zone des Amm. Sowerbyi," has traced in a general way, following out simply the physical features of the distribution of the Jura, the following basins: I. South German Basin, consisting of Suabia, Franconia in Bohemia, and southeastern Baden "und des Randen." II. Helvetic Basin, including Switzerland, departments of Doubs, Jura, and Ain, also Rhone, Saone et Loire, Côte d'Or, Haute Saône, Haut Rhin, and Bas Rhin, and the neighboring deposits in the south of Baden. III. Mediterranean Basin, including the departments of Lozère, Aveyron, Hérault, Gard, Ardèche, Drôme, Basses Alpes, Var, and Bouches du Rhone, and suggests an Italian basin for the Southern Alps. IV. Pyrenean Basin, including the departments of Lot, Charente, Charente Inférieure, and perhaps Deux Sèvres. V. Parisian Basin, including the depart-

<sup>&</sup>lt;sup>1</sup> The use of the word zone instead of band is likely to lead to confusion, on account of its employment in geology for the synchronous faunas of the same beds, and we think it ought to be avoided.

ments to the north, to which Waagen adds Dorsetshire and Wiltshire in southern England. VI. North English Basin, from Gloucestershire to Yorkshire inclusive. VII. North German Basin, including Hanover, Brunswick, and the neighborhood of Magdeburg.

We have not needed to use these divisions precisely as laid down by Waagen, but it is interesting to remark that they accord more or less completely with the observations on the faunas here recorded. Our principal interest has been, of course, in the central portion of each basin, and not in the more deficient records of outlying localities. The South German basin is as it has been given by Waagen. His Helvetic basin appears to be a natural division, with the exception of the departments of Saone et Loire, the Côte d'Or, and the Rhone. The Côte d'Or has appeared to us to be the centre of a different basin, which extended indefinitely through the departments to the westward, and also to the south until it met the fauna in the valley of the Rhone described by Dumortier. Whether such closely contiguous faunas as that of this valley and the Côte d'Or ought to be designated by distinct names we cannot pretend to decide, but that they differ materially from the point of view of the evolution of their faunas seems to us highly probable.

The faunas of northeastern France and Luxemburg, though perhaps in a distinct basin from those of Westphalia, Hanover, etc., which are properly included in the North German Basin, are all similar in so far as they contain similar residual faunas. The basin of the Rhone includes the departments mentioned as in the Mediterranean basin by Waagen, with the exclusion of the southeastern part of the department of Var, which, as shown by Dieulefait, belongs to the Italian basin. We have not been able to study any collections from Wiltshire, but the Dorsetshire fossils of the Lower Lias, though certainly presenting a very distinct facies and association of forms from those of Waagen's North English basin, have not seemed to require separation into a different basin. The fossils do not resemble those of any other fauna so closely as they do that of the rocks in the rest of England to the northeast, and, though it may be natural to make this separation, we have not required it for the immediate purposes of this memoir, and have consequently spoken of the entire region as the English basin.

The Lias in territories to the north, like Scotland and Sweden, is deficient in Ammonitine, and Judd¹ remarks upon the estuarine character of the deposits. At Dompau and Döshult in northwestern Sweden a few poorly preserved fossils show the presence of the bucklandian fauna. It is possible that these deposits may have a yet undiscovered fauna of Ammonitine distinct from more southern localities; but so far as one can see, the forms of the Swedish basin are not distinct from those of the faunas of North Germany.

Neumayr has already traced in a general way the origin of the fauna of Central Europe to the Mediterranean province, and we think a still further advance has been made practicable by the methods of constructing genetic series as advocated in this monograph, and the discovery of definable cycles in the genesis of forms. Though our conclusions have been reached under the dis-

<sup>&</sup>lt;sup>1</sup> Quart. Journ. Geol. Soc. London, 1873, XXIX. p. 98.

advantages attending residence at a distance from the fields of research, the results have appeared to be sufficiently novel and suggestive to warrant publication. The results reached have been just what one might have anticipated from a priori reasoning upon the basis of the theory of evolution and monogenesis, but nevertheless have not been admitted without much hesitation, because of the author's natural feeling that so great exactitude in statement with regard to the relative age of faunas on the same horizon should be distrusted.

If our data have led us correctly, there are some basins in the Lower Lias which were capable of evolving new forms. These we have called Aldainic Basins, because they were centres of origin for new series, and their faunas were what we have called Autochthonous Faunas. Other basins were apparently incapable of giving origin to new forms, or at any rate received all, or almost all, the forms which occupied their territory by migration from the aldainic basins. These we have called Analdainic or Residual Basins, and their faunas Residual or Analdainic Faunas. The beginning of the Arietidæ was in the Northeastern Alps, and this, being the first autochthonous fauna, was older than all others. Thence South Germany or Suabia was peopled by chorological migration, and then the basin of the Côte d'Or. Thus a Zone of Autochthones, or an aldainic band of basins, was formed running to the westward. North and south of this zone all faunas seem to have been residual faunas.

The fauna of the Lower Lias in the basin of the Northeastern Alps was, however, not in the zone of autochthones after the deposition of the Angulatus bed. This zone, just before the deposition of the Lower Bucklandi bed, had become narrowed in its easterly extension, and confined to the faunas of South Germany and the Côte d'Or.

# PSILOCERAS AND CALOCERAS.

The discovery by Gümbel<sup>2</sup> of *Psil. planorboides* in the triassic strata of the Bavarian Alps having been confirmed by Winkler<sup>3</sup> and the shell and sutures figured, there can be no doubt that it is a true Psiloceras. As a result of our researches upon cycles of form, we can, however, unhesitatingly assume that this shell is too involute to be considered a radical of the Arietidæ. It indicates, if estimated according to the usual history of these cycles, that undiscovered species of discoidal Psiloceratites must have existed in the Trias, as necessary antecedent or ancestral forms. Two forms have also been cited by Neumayr, in his "Unterster Lias," as *Egoc. planorboides* and *Egoc. form. nov.* from the Kössener shales. These are from Wallegg, and appear to be the same as those previously cited by Stur<sup>5</sup> as *Amm. ef. longipontinus* and later described by Wähner.<sup>6</sup> Wähner considers them both to be specimens of his *Psil. Rahana*, and writes that

<sup>1 &#</sup>x27;Aλδαίνω, to make to grow. 
<sup>2</sup> Ober. Abth. d. Keupers, p. 410.

<sup>&</sup>lt;sup>8</sup> Zeits. deutsch. geol. Gesellsch., 1861, XIII. p. 489, pl. ix. fig. 3. Neumayr also, Unterster Lias, Abhand. geol. Reichsans., VII., figures this species in the Planorbis bed.

<sup>&</sup>lt;sup>4</sup> Abh. geol. Reichsans., Wien, VII. p. 44.

<sup>&</sup>lt;sup>5</sup> Fuhrer z. d. Excursion. d. deutsch. geol. Gesellsch., Wien, 1877, p. 148.

<sup>&</sup>lt;sup>6</sup> Verhand. geol. Reichsans., 1886, p. 175.

they were probably taken from loose rock not in place, and may have come from a dark gray limestone in the horizon of *Psil. caliphyllum* or *megastoma*. They cannot, therefore, be considered forerunners of the psiloceran forms of the Planorbis bed.

Neumayr's and Wähner's researches, quoted below in Table VI. and in the chapter on "Descriptions of Species," show that a wonderfully rich fauna of Psiloceratites and Caloceratites existed in the region of the Northeastern Alps; but, so far as we know, there is nowhere any statement of the appearance in time of the discoidal radical Psil, caliphyllum or planorbe before Caloceras in that province, as there is in South Germany. The aspect of the fauna is older than that of South Germany; but though composed of an assemblage of radical forms of Psiloceras, they occur side by side with Cal. Johnstoni and Schlot. catenata (subangulare of Wähner), and are equivalent to the fauna of the Caloceras bed of South Germany, but not to the lowest Planorbis bed. Suess and Mojsisovics, in their table of strata in the mountains of the Osterhornes, Northeastern Alps, describe a very thick Planorbis horizon, and in the uppermost bed they enumerate Psil. planorbe, supposed to be the English form; also Psil. Hagenowi and Cal. Johnstoni, no fossils having been found in lower beds. Here again it is probably the Caloceras bed, and not the lowest Planorbis bed, which contained the fossils described.

In South Germany *Psiloceras planorbe*, the radical species of the Arietidæ, is prevalent, as may be seen in collections, and in the works of all the geological writers on this region, especially Quenstedt. Quenstedt notes what he calls the Laqueum layer, and speaks of caloceran forms as having made their first appearance somewhat later in the Planorbis horizon than *Planorbis* itself, and in the "Ammoniten der Schwabischen Jura" describes and figures a specimen, *Planorbis*, var. *leve*, from the Bone-bed, which is placed by most writers in the Rhætic.

In the neighborhood of Salin and Besançon, Prof. Jules Marcou has shown that there is a deficiency in the Planorbis horizon, and lately Louis Rollier, following in his footsteps, has confirmed these observations. Professor Marcou, however, at Boisset, near Salins, found a true Planorbis bed containing the typical species. W. A. Ooster, in the "Catalogue des Cephalopodes des Alpes Suisses," enumerates many species; but unluckily the beds are not defined. It is, however, evident that the collections in Switzerland which he examined, and the authors he quotes, did not give any data contradictory to Waagen's conclusions, which we give below.

Waagen, in his "Der Jura Franken, Schwaben und der Schweiz," says that outside of Suabia, whether going northeast or southwest, one finds nowhere the typical development of the Lower Lias as it exists in Suabia; and it is especially the lowest bed which is apt to be nearly everywhere starved out. This remark and the table given by Waagen are very important, and coincide with the results reached in this chapter.

<sup>&</sup>lt;sup>1</sup> Gebirgesg. d. Osterh., Jahrb. geol. Reichsan., XVIII., 1868, p 195.

<sup>&</sup>lt;sup>a</sup> Form. Jurass. Soc. d'Emulat. Porrentruy, 1883, p. 105.

<sup>&</sup>lt;sup>2</sup> Denksch. schw. Gesellsch. Naturwissen., XVIII., 1861.

M. Collenot mentions Amm. Johnstoni, tortilis, laqueum, and Burgundiæ as occurring in the Planorbis horizon. The collections at Semur show that Planorbis was small, and evidently already losing ground, whereas the fine suites of caloceran fossils indicate at least that this series had suffered no loss by migration when compared with the fauna of South Germany. This collection is also arranged to show a bed similar to the Laqueum layer of Quenstedt, called by Collenot the "zone of Amm. Liasicus," which contains only caloceran forms, and also Psil. longipontinum. Cal. laqueum is smaller, and more like the German form when found in company with Liasicus.<sup>2</sup> A few dwarfed forms of Psil. planorbe, var. leve, have been found together at Saulieu, and at Beauregard there is a bed with large forms of Cal. Johnstoni and tortile, accompanied by a larger form of Cal. laqueum than is usual in South Germany, and a small Psil. planorbe, var. leve. The latter is in Boucault's collection, Museum of Comparative Zoölogy, but not represented at the time of my visit in the collections at the Museum of Semur. The researches of M. F. Cuvier<sup>3</sup> are important in this connection. He states that a separable Planorbis bed was found by him on the section of the railway between Arcy-sur-Cure and Guillon, and immediately above this a bed characterized by the presence of Cal. Liasicum. Again, on page 177, he speaks of finding at Gravelles, near Saulieu, a bed containing Psil. planorbe and Cal. laqueum or Buraundia, and this agrees with Collenot's observations.

Dumortier <sup>4</sup> states that *Psil. planorbe* occurs everywhere in the Planorbis bed of the basin of the Rhone in company with *Cal. Johnstoni*, though not an abundant fossil, and from a fragment in his possession infers that the former may in some cases have reached the great diameter of 220 mm. Quenstedt describes and figures a specimen of *Psil. planorbe*, var. *leve*, from Provence, <sup>5</sup> which he names *Amm. psilonotus provincialis*. Martin <sup>6</sup> designates the Planorbis bed in the region of the Côte d'Or as the "zone of *Amm. Burgundiw*" (our *Cal. laqueum*). He considers that the beds of "lumachelle," the Planorbis horizon, show evidences of having been deposited during a period of violent currents, etc. This is an important fact, since it indicates the littoral character of the deposits.

Terquem,<sup>7</sup> in the department of Moselle, writes that Ammonites are generally rarer and more often broken than Nautili in the Lower Lias, and enumerates only six species. Chapuis and Dewalque state <sup>8</sup> that in Luxemburg the Planorbis zone is not fossiliferous.<sup>9</sup>

Description Géologique de l'Auxois, p. 209.

<sup>2</sup> The remarks of M. Collenot on page 164 are very instructive, and confirm the impressions received from the collections at Semur.

Notice Géologique, etc., Bull. Soc. de Semur, ser. 2, No. 3, 1886, pp. 170, 176.
Étude Paléontologique du Bassin du Rhone, p. 28, pl. i.

<sup>5</sup> Amm. Schwab. Jura, pl. i. fig. 19.

6 Pal. Strat. de l'Infra-Lias de la Côte d'Or, Mém. Soc. Géol. de France, VII.

7 Infra-Lias Luxem., etc., Dept. Moselle, Mém. Soc. Géol. France, V. See also, for similar opinions, Collenot, Descr. Géol. de l'Aux., p. 162, and Dumortier, Études Pal. Bass. du Rhone, I. p. 20, II p. 97.

<sup>8</sup> Descr. Foss. Terr. Secon. de Luxembourg.

9 The late researches of Schumacher, Steinmann, and Van Werveke, Erlaut. z. Geol. Uebersichtsk. d. Westl. Deutsch-Lothringen, show that the Planorbis bed containing Psil. planorbe, var. plicatus, is found in the region explored by them, though it is absent in the French part of Lothringen, as stated by Bleicher, Bull. Soc. Géol. de France, ser. 3, XII., 1884, p. 445. In Deutsch-Lothringen it is one meter in thickness.

In North Germany, according to Schlönbach,1 the Planorbis horizon is present; but Psil. planorbe is largely, if not entirely, replaced by Cal. Johnstoni, and he designates this layer as the "zone of Amm. Johnstoni." Braun 2 gives similar results for his work in the localities of northwestern Germany; and Emerson, in his essay "Die Liasmulde von Markoldendorf," did not find Psiloceras in that basin, though Johnstoni was abundant, and of large size. Römer,3 the first observer in North Germany, states that the Lower Lias is less developed in that region than in South Germany, and enumerates only a few species. Schlüter, in his "Schichten des Teutoburger Waldes bei Altenkirchen," shows that a thick Planorbis bed occurs in this locality, and Psil. planorbe is abundant, while Cal. Johnstoni, which he considers to be identical with planorbis, var. plicata, and Amm. luqueolus, is much less frequent.4 He also gives Amm. angulatus as appearing in the upper part of the same bed. There is unfortunately no record of the exact beds in which the fossils occurred, and it is not certain, therefore, whether we are here dealing with the Caloceras bed or a true Planorbis bed. Quenstedt also describes and figures a specimen of Psil. plunorbe, var. leve, from Quedlinburg.5

The paleozoölogical and geological data, therefore, appear to sustain the conclusion, that Psiloceras and Caloceras, as a rule, arrived later in North Germany and Luxemburg, the Côte d'Or, and the Basin of the Rhone, than in South Germany.

In England the aspect of the fauna has greater similarity with the Côte d'Or and South Germany, than with the North German and Luxemburg basins. The Planorbis zone is well developed, and in the Bristol Museum the South German varieties of Psil. planorbe and the English forms from Cotham 6 are found side by side. This was also the richest collection in caloceran species which we saw in England, though it was still far behind that at Semur. Rev. J. E. Cross, in his "Geology of Northwestern Lincolnshire," claims that no true Planorbis bed occurs, but in place of this a bed containing Amm. angulatus and Johnstoni, which is probably the Caloceras bed. Wright's section at Uphill railroad cutting shows the bed containing "angulatus and fragments of Liasicus," called by him the "Angulatus bed," and at Binton, Warwickshire, there is a transition bed containing only Liasicus, included by him in the Planorbis zone.7 In his sections of the Planorbis horizon Psil. planorbe occurs earlier than any species of Caloceras at the Uphill railroad cutting; at Binton, Warwickshire; Street, Somerset; and at Brockeridge and Defford Commons. No mention, however, of Psiloceras in any earlier bed occurs, and its appearance must therefore have been later, as a rule,

<sup>2</sup> Der untere Jura in nordwestliche Deutschland, 1871.

<sup>3</sup> Verstein. norddeutsch. ool. Geb.

<sup>4</sup> Zeits. deutsch. geol. Gesellsch., 1866, XVIII. p. 40.

<sup>5</sup> Amm. Schwab. Jura, pl. i. fig. 17.

<sup>&</sup>lt;sup>1</sup> Ueber Eisen, d. Mittl. Lias, etc., Zeits. d. geol. Gesell., 1863, p. 498; Paleontogr., XIII.; and Die Hannoverische Jura, p. 17.

<sup>&</sup>lt;sup>6</sup> Stoddart, in his "Notes on the Lower Lias of Bristol," Geol. Mag., V., 1868, p. 139, shows that Amm. Johnstoni occurs in the section he described earlier than true planorbis, if one can judge from the names he gave to the beds, since no lists of fossils were added. The section given certainly indicates the existence of a Caloceras, rather than a true Planorbis bed.

<sup>7</sup> Wright, Lias Amm., pp. 11, 20.

than in South Germany. Tate and Blake i discuss the conditions of the deposition, and arrive at the conclusion, that "it seems probable that no portion of the liassic beds was formed in very deep water, but that even the shales partook of the nature of submerged mud flats."

Psil. Hagenowi occurs in the Northeastern Alps, North Germany, Bohemia, and Switzerland; and in all these places the true Psil. planorbe, var. leve, is scarce. This form is a degraded modification of planorbe which may have arisen independently in each locality, and it indicates that this species probably lived under unfavorable conditions in these regions. Caloceras was, however, strongly represented in the same basins. It formed an unbroken procession, so far as Cal. Johnstoni was concerned, from the Northeastern Alps to England.

The facts, with certain exceptions, of which we shall take note farther on, appear to indicate that Psiloceras was autochthonous in the Northeastern Alps. It probably appeared as a radical or chronologic migrant from the Trias, and gave rise to Caloceras in the Lias. Thence both series may have spread by chorological migration into the basins of South Germany, the Côte d'Or, Switzerland, North Germany, and England. During these migrations they met with favorable conditions in some localities, and unfavorable conditions in others; hence the inequalities of representation. In both series, however, it is obvious that it was the discoidal species which settled in the new territories to the west of the Mediterranean province. It thus becomes evident that the more highly specialized and more involute species were probably not the progenitors of any of the derivative series that subsequently arose, — an inference agreeing exactly with all our conclusions with regard to the radical nature of discoidal, as compared with involute forms.

#### Wæhneroceras and Schlotheimia.

The exceptionally rich fauna of the Angulatus (Megastoma) bed given by Wähner<sup>2</sup> contains, besides the distinctive Wæhneroceran series, Schlot. angulata, and other forms of the same series, as well as many of the involute Psiloceratites and keeled Caloceratites, mentioned above. This assemblage shows undoubtedly that a region so richly populated must have been exceptionally favorable for the evolution of Wæhneroceras, and possibly also the autochthonous home of Schlotheimia. The announcement by Neumayr<sup>3</sup> of Waagen's discovery of a true Schlot. angulata in the Rhætic beds near Parthenkirchen in the Mediterranean province, should be mentioned in this connection. Suess and Mojsisovics show that the Angulatus zone is very slightly developed in the Osterhornes mountains, but it contains Psil. longipontinum, Cal. laqueum, Schlot. angulata and Moreana, besides a possible Cor. kridion, identified as similar to that figured by Dumortier in France. This assemblage, therefore, contains the most important of the species found in other regions in the Caloceras bed, as well as in the true Angulatus bed above.

Yorkshire Lias, p. 215.
Unter Lias, loc. cit., IV., 1886, p. 199.

<sup>&</sup>lt;sup>8</sup> Jahrb. geol. Reichsans, 1878, XXVIII. p. 64, and Abh. geol. Reichsans., VII. p. 44.

The radical form Schlot. catenata appeared in the Planorbis horizon, according to the collection at Semur, and in this fauna the successive forms of the schlotheimian series succeed one another without a break in their gradations. Quenstedt's work on "Die Ammoniten des Schwabischen Jura" shows that in South Germany the series may be complete in numbers of forms, and even more remarkable in the size of specimens, and the whole series except Boucaultianus appeared before the termination of the Angulatus fauna. There is also a specimen referred doubtfully even to the "gelbe Sandstein" of the Rhætic beds near Tübingen, thus carrying the possible origin as far back as in the Northeastern Alps. If, as we have supposed, Wæhn. subangulare is found in South Germany, the evidence becomes still stronger that this was the probable centre for the chorological distribution of the group in Central Europe.

Schlot. angulata and cutenata are very numerous in North Germany; but there is a notable tendency to the production of smaller specimens in the collections we have seen. Schlüter, in his "Schichten des Teutoburger Waldes bei Altenbecken," states that Amm. angulatus, Moreanus, and Charmassei occur there, but that the latter is never so large as in South Germany.

Terquem, in his "Province de Luxembourg et de Hettange," mentions Amm. angulatus as occurring in abundance, and of good size, but no species like Charmassei or Leigneletii. Chapuis and Dewalque give figures of Schlot. angulata, which show that the species is similar to catenatus in having discoidal whorls and the pilæ crossing the abdomen. This species is evidently similar to that from Markoldendorf, described by Emerson. Seebach, in his "Hannoverische Jura," declares that in North Germany there has so far been found only the Amm. angulatus (equal to depressus, catenatus, and Moreanus), and denies the existence of Charmassei. Brauns, in his "Untere Jura im nordwestlichen Deutschlands," cites both angulatus and Charmassei.

The whole series, including radical, discoidal, and involute species, appear to have come into the Northeastern Alps basin first, and to have reached in this locality their highest development in discoidal forms. Thence they seem to have spread somewhat later in time into the Angulatus horizon of the South German basin, and migrated still later to the Côte d'Or and England. In the first two basins they reached their highest development in involute forms, a fact which strengthens the impression that the series must have originated in the Mediterranean province, since the involute forms are the descendants of the discoidal forms. That they arrived in the Côte d'Or later than in South Germany is shown by Tables I. and II., in which we find Charmassei appearing in the Lower Bucklandi zone instead of the Angulatus zone, and by the presence of two new and more highly modified species, D'Orbigniana and Boucaultiana, which have not been found in South Germany by any collector up to the present day. These views are further sustained by the fact that the English fauna possesses only a slender representation of the group, all the species being rare, and occurring at about the same time as in the Côte d'Or, except Boucaulliana, which is

<sup>&</sup>lt;sup>1</sup> Page 42.

<sup>&</sup>lt;sup>2</sup> Mém. de la Société Géol. de France, V.

<sup>&</sup>lt;sup>3</sup> Descrip, Foss, Terr. Secon. de Luxembourg.

found somewhat earlier in the Upper Bucklandi bed. Neither Schlot. D'Orbigniana, nor any of the similar modifications so well exhibited in the collections at Semur and in the Boucault collection of the Museum of Comparative Zoölogy, are represented in this fauna.

#### VERMICERAS.

Vermiceras is represented in the Northeastern Alps by Ver. Conybeari, figured by Hauer, and Ver. Hierlatzicum, Geyer, a dwarfed species. Amm. spiratissimum, Hauer, occurs in company with Conybeari in the Lower Bucklandi bed at Enzesfeld; but this is probably a species of Caloceras, similar to Cal. carusense, of the large variety which occurs in the Bucklandi horizon in South Germany.

Suess and Mojsisovics do not give any species of this genus as occurring in the Osterhornes mountains, and this is also the case in several other localities where the formations are sufficiently well developed to lead one to expect that the genus would be represented if at all common in this province. Cal. prespiratissimum, in the Angulatus bed of the Kammerkahr Alps and Adneth, as given by Wähner, is the only example of a transitional form. Nevertheless the great development of caloceran species in the Mediterranean fauna shows that a complete series of transitional forms probably occurred in that province.

Gümbel does not mention Vermiceras, in his "Geognostische Beschreibung der Bayerischen Alpen," as having been found in the Kammerkahr Alps, unless indeed his Amm. spiratissimum is a true vermiceran form, or similar to Wähner's species of prespiratissimum, nor did he find any species of this series in the gray limestones at Gastätter Grabens. Herbich, in his "Széklerland," gives figures and descriptions of Arict. multicostatus, with both young and adult similar to and probably the same as his Arict. Conybeari, all having been found near Also Rakos in the Besanyer mountains. The radical species Ver. spiratissimum made its appearance in South Germany earlier than elsewhere, if we can regard, as seems to us correct in every way, transitional forms like that on Summ. Pl. XI. Fig. 22, though named as belonging to Cal. laqueum, as really closer to Vermiceras than to Caloceras. The principal transitions must have taken place in the Caloceras bed of this basin, instead of in the Angulatus bed, as in the Mediterranean province.

The basins of South Germany and the Côte d'Or are about equivalent in the number of transitional forms, and it is as easy to trace the gradations from Caloceras to *Ver. spiratissimum* in one locality as in the other. The extraordinary evolution of the series in the Côte d'Or indicates that it must have met with its most favorable home on the bucklandian horizon in this basin. Even on the Tuberculatus horizon several new varieties were evolved, some of which, however, like *debilitatus*, Rey., must be considered as degradational, and consequently indicate the decadence of the genus in this later fauna.

According to Dumortier's figures and descriptions, this genus is represented

<sup>&</sup>lt;sup>1</sup> Mojsis. et Neum., Beitr., V. p. 53.

<sup>&</sup>lt;sup>2</sup> Mittheil. Jahrb. d. k. ungar. Geol. Anstalt., V., Part II.

by very few forms in the basin of the Rhone, and Ver. spiralissimum appeared first in the Lower Bucklandi bed.

In England the number of varieties or forms is not equal to either of the three faunas above mentioned, but the transitional forms are present. Wright, in his "Lias Ammonites," gives a section at Red Car, and Amm. Conybeari is cited as occurring in the lowest stratum of the Bucklandi zone. With regard to the English fauna, one can see, in spite of the large size and the multitude of specimens, that the small number of distinct species and the entire want of autochthonous species, or varieties, indicate a purely residual fauna composed of unmodified forms. This basin is north of the zone in which autochthones arose during the Lower Lias, and the basin of the Rhone lies south of this zone, and both are residual faunas. Ver. Conybeari is mentioned by several authors as occurring in North Germany and in Luxemburg, but, so far as we have seen, other forms of this genus have not been cited, and Vermiceras appears to have had but slight development in these basins

The facts, so far as now known, are opposed to the inference that this series originated in the Northeastern Alps. On the contrary, it seems more likely that it began in the Caloceras bed of South Germany with a variety of Cal. laqueum, and subsequently appeared as Ver. prespiratissimum in the fauna of the Angulatus zone in the Mediterranean province. The series, however, did not, either at this time or on any subsequent horizon in this province, meet with very favorable conditions for the evolution of new forms. It must be remarked, also, that the variety of Conybeari figured by Hauer and by Herbich has a whorl quite distinct from that which occurs most commonly in Central Europe. It is more like the degenerate variety of Conybeari, which is usually called Bonnardi, though apparently of smaller size.

## Arnioceras.

There are quite a number of forms described by various authors as having been found in the Mediterranean province, but they have all been found in horizons above the Lower Bucklandi bed. This may be seen by our Table VI., and also in the fact that Suess and Mojsisovics found no species of this genus in the Osterhornes mountains, the beds above the Bucklandi zone being unfossiliferous, and Paul states, in his article "Die Nördliche Arva," that only one species of this series was found in the Lias, and this occurred in the beds above the Bucklandi zone.

My notes on the collections at Stuttgardt and Tübingen do not show so rich a fauna as in the Côte d'Or, nor do Quenstedt's publications indicate so full a development of the series as in that basin. Thus, though the series began in the Angulatus zone, as shown in Fraas's collection, it did not reach its acme of development in the South German basin. The evolution of Arnioceras in the fauna of the Côte d'Or is exhibited in the Semur collection, and in Boucault's collection of the Museum of Comparative Zöology. The large number of forms in

<sup>&</sup>lt;sup>1</sup> Jahrb. geol. Reichsans., XVIII., 1868, p. 233.

the bucklandian horizon, and their early appearance in the Angulatus zone of Côte d'Or, show that this was their most favorable home. We have identified the earliest occurring Semur specimen with Arn. falcaries, but it had some transitional characters allying it with Arn. miserabile and also with Arn. semicostatum. Arnioceras did not appear at all in the Angulatus zone, but in the Bucklandi zone of the Rhone basin, if Dumortier's work can be considered as authoritative upon this question. This fauna also possesses specimens of much larger size than any found elsewhere, and the series is quite as fully, though perhaps not so richly, represented as in the basin of the Côte d'Or.

In England there are certainly fewer species and forms than in South Germany or the Côte d'Or, and they appear to have been wholly migrants, not possessing the numerous varieties observable in South Germany and at Semur.

Only one, or at most two, species of Arnioceras, called either obliquecostatus of Zeiten, or geometricus after Oppel, appear to have been found in North Germany. Making all due allowances for negative evidence, this appears to indicate a very slight representation of the genus. Schlüter gives, however, a lengthy description and figures of Amm. obliquecostatus as occurring in a bed between the Angulatus and the Bucklandi zone in the Teutoburger Wald, and his description and figure show that this species may be in reality divisible into several,—one similar to Arn. oblusiforme, one to miserabile or semicostatum, and perhaps another with more marked keel and channels. The forms are confined wholly to this stratum, which may belong either to the Angulatus or the Bucklandi bed. The Luxemburg fauna was equally poor.

This genus, therefore, certainly does not have the aspect, as far as is now known, of having originated in or near the basin of the Northeastern Alps. The evidence is rather in favor of its having arisen from small planorbis-like forms, occurring first either in the Côte d'Or or in the South German basins. At present the evidence is not determinative, though somewhat in favor of the former basin. The series subsequently migrated to the Mediterranean province, making its first appearance there in the Upper Bucklandi zone.

#### CORONICERAS.

In company with the first arnioceran species at Semur is a doubtful form of Cor. kridion, and later in the Scipionis bed a true Cor. kridion is found together with a representative of Cor. rotiforme. Cor. latum also occurs in company with these, but is the radical of another subseries of this genus. Cor. kridion is cited by Suess and Mojsisovics from the Osterhornes mountains as occurring in the Angulatus zone, and this is not a difficult species to identify. The Coroniceran forms as cited by the same authors in the Bucklandi zone are represented only by Cor. bisulcatum. Hauer's work, however, shows that this is probably only a local peculiarity, though the fauna is not so rich as that of either South Germany, France, or England.

Dumortier, in his "Études Paléontologiques du Basin du Rhone," gives Cor.

kridion as occurring in the Angulatus beds, and figures a specimen. According to Fraas's collection, Cor. kridion certainly appeared in South Germany in the Angulatus bed at Möhringen, and Quenstedt declares it to be a rare form in the Bucklandi zone. Coroniceran forms are so numerous in the Bucklandi zone of South Germany and France, that it becomes difficult to determine whether they were more fully evolved in the one or the other of these basins.

Wright's tables and lists show that the English fauna was by no means so rich in numbers of species and varieties as either the French or South German; and this result, notwithstanding the great size and multitude of specimens found in the various localities of that basin, confirms our experience in the study of collections while in England.

The works of North German paleontologists show less thinning out of the forms of this series in that direction than in any of the preceding genera. The names bisulcatus, multicostatus, and the like, occur frequently. This suggests that in bucklandian times the species of the Arietidæ had become hardier and more able to survive in the unfavorable localities to the northward, or else the surroundings themselves had changed and become more favorable. There is one fact, however, favoring the former as the most probable conclusion. The specimens are neither very abundant, nor are they so large, nor so generally distributed in North Germany as in South Germany.

The radical of the third subseries of Corniceras, Cor. Sauzeanum, did not appear earlier than the Upper Bucklandi bed in any fauna, not excepting that of the Mediterranean province.<sup>2</sup> Chapuis and Dewalque show that Cor. Sauzeanum persisted in the Luxemburg region, and that Cor. bisulcatum and multicostatum were also present; but the number of forms found there are certainly very limited. Schlönbach mentions the usual fauna of the Bucklandi zone in Brunswick, but the species are not so numerous as in South Germany, and no note is made of their abundance. The absence of the Tuberculatus bed, or its unfossiliferous character when present, is noted by Schlönbach, and this indicates a decrease in number of forms as compared with other regions. Brauns in "Hannoverische Jura," and Emerson in "Liasmulde von Markoldendorf," show that the coroniceran series is represented, but is not remarkable for the number of species, and in most localities, so far as we can learn, the species of this series are not abundant. Shlüter cites Cor. rotiforme and Cor. Gnuendense as occurring in the Bucklandi zone of the Teutoburger Wald, and his descriptions support these results. He alludes to other forms than these species, but does not enumerate them.

The poverty of the later beds of the Lower Lias in North Germany, and the constant recurrence of unfossiliferous strata, are characteristics similar to those of the basin of the Northeastern Alps, and these facts indicate that similar unfavorable conditions obtained there.

Dumortier's work enables us to see, also, that in the Rhone basin on the southern side of the Côte d'Or the fauna thinned out. Thus, though Cor. kridion

<sup>1</sup> Pl. xviii. fig. 3, 4.

<sup>&</sup>lt;sup>2</sup> See Mojsisovics's mention of the zone of Amm. Sauzei, Gebirgsgr. d. Osterhornes, p. 199.

appeared in the Angulatus zone, the number of species on the bucklandian horizon was evidently more limited than in South Germany, Semur, or England.

The coroniceran series, therefore, seems to have arisen on the same level in the Mediterranean province, in the South German basin, and probably in the Côte d'Or. The radicals of the subseries, so far as known, do not follow the same law. Cor. latum has not yet been mentioned or described as occurring in any other basin than the Côte d'Or. Cor. Sauzeanum occurs, however, in northwestern Germany, according to Braun, and in the South German, Côte d'Or, and English basins in the Upper Bucklandian bed, though in the basin of the Rhone and Mediterranean province it is not recorded with certainty from any level earlier than the Tuberculatus beds.

It is possible that Cor. kridion may have originated in the Northeastern Alps, but Neumayr and Wähner have not yet found this species in their researches among the fossils of the Angulatus zone, and no good figure has been published. The early occurrence and large number of varieties and species in the collections at Stuttgardt and Semur, and the numerous transitional varieties, also show that Cor. kridion found its most favorable home either in the South German or the Côte d'Or basin. The earlier occurrence of the radical of the third subseries, Cor. latum, at Semur, indicates the Côte d'Or to have been the centre of distribution for the Bucklandi subseries. The occurrence of Cor. Sauzeanum on the same level in South Germany, Côte d'Or, and England shows, together with the number and variety of the forms subsequently evolved, that the centre of distribution of the Bisulcatus subseries lay in one or the other of these basins.

This conclusion accords with the origin and distribution of the parent series, Arnioceras, and derives additional support from this fact. It is evident also, from these facts, that the Mediterranean province must be regarded as having been peopled with migrants from the province of Central Europe, so far as relates to the subseries of this genus, and this makes it more likely that the radical species of the whole series, Cor. kridion, also arose in this province. So far as known its appearance in the Angulatus horizon of the Northeastern Alps is not supported by the presence of transitional forms, nor by the presence of Arnioceras in the same horizon. The species, if a real kridion, certainly must be provisionally regarded as a chorologic migrant from the west.

## Agassiceras.

Agas. lævigatum appeared in the Angulatus zone of the Semur collection, and was represented by numerous specimens in this fauna. It is also attributed to this horizon in the basin of the Rhone by Dumortier, and is well figured by him.¹ In South Germany Agas. lævigatum did not appear until the Upper Bucklandi bed. In England and North Germany it appeared associated with planicosta above the Bucklandi horizon. This radical species, therefore, according to our present knowledge, was a migrant in all of these basins, derived probably from the Côte d'Or or the Rhone basin.

<sup>&</sup>lt;sup>1</sup> Études Pal., pl. xviii. fig. 5, 6.

Neumayr<sup>1</sup> includes what we consider the young of the radical species of Agassiceras in his genus Cymbites, and states that he has not found them in the basin of the Northeastern Alps. Geyer, in his "Cephalopoden Hierlatz-Schichten bei Hallstadt," figures and describes under the name of Cymbites a characteristic young form of Agas. lævigatum. Hauer's drawings of Amm. abnormis, in his "Unsymmetrische Ammoniten der Hierlatz-Schichten," illustrate typical shells belonging to the compressed variety of the same species, one of them exhibiting the peculiar aperture, and another the gibbous young in the interior. The radical species of the series, therefore, appeared in the Northeastern Alps not earlier than the Upper Bucklandi beds, as in other faunas more or less remote from the Côte d'Or.

In the next subseries we find that Agas. Scipionianus and Scipionis are characteristic fossils of the Lower Bucklandi bed in the Côte d'Or and Rhone basins, but in South Germany and England they appeared later, together with Agas. striaries in the Upper Bucklandi bed, and in North Germany on the same horizon. So far as known, no species of this subseries has been found in the Northeastern Alps.

This series, therefore, has the aspect of having first appeared and met with a favorable home in the Côte d'Or or the basin of the Rhone, where its immediate radicals are found.

#### ASTEROCERAS.

The asteroceran series is represented in the Northeastern Alps, though apparently not by many forms. Hauer figures an Ast. obtusum, var. stellare, and we have seen several specimens from this region, but the fauna evidently was not a rich one as compared with those to the westward. According to Suess and Mojsisovics, this species does not occur earlier than the Obtusus bed 2 in the strata of the Osterhornes mountains, the Adnether-Schichten in which it appears being placed by them above the Tuberculatus bed. According to our classification, however, this curiously mixed fauna may have begun to receive migrants from the west during the time of the lower bucklandian horizon.<sup>3</sup>

The first recorded appearance of Ast. obtusum occurred in the Upper Bucklandi bed of South Germany, and in the similar formation of Luxemburg.

M. Collenot, in his table of the forms in the Côte d'Or, quotes only the usual three names, Amm. obtusus, stellaris, and Brooki. Boucault's collection in the Museum of Comparative Zoölogy shows, however, that probably all the principal forms were present in the basin of the Côte d'Or, and the type of Ast. Collenoti was certainly found there. Dumortier shows in his work, that this species was also present in the Rhone basin, but the series of forms in the genus was not otherwise so complete as in the Côte d'Or. The finest series exists in the collection at the Museum of Stuttgardt. This does not have Collenoti, though it

<sup>&</sup>lt;sup>1</sup> Ueber unvermit. auftret. Cephalopodentypen, pp. 63-65.

<sup>2</sup> Op. cit., p. 198.

<sup>&</sup>lt;sup>3</sup> The form cited by Wähner, Ariet. stellæformis, an ally of Ast. obtusum, var. quadragonatum, is cited as having been found in the Megasoma or upper part of the Angulatus beds in the Kammerkahr Alps. This is a doubtful matter, since only one specimen exists, and we have therefore allowed the text to stand as written (Wähner, Mojsis. et Neum., Beitr., VI., pl. xxvi., 1888). See also description of this variety, Chapter V.

does possess Ast. acceleratum, a form found nowhere else except in the Côte d'Or. Quenstedt's collection at Tübingen is very fine, and his descriptions and figures indicate a full representation of species, though Collenoii is not present.

Chapuis and Dewalque show that the Luxemburg rocks contain several different forms of the genus, though they are not so numerous as in South Germany or England. Schlönbach shows that there is an *obtusus* horizon in North Germany containing the usual forms, but only fossiliferous in certain localities, and Brauns publishes similar results in his work. This horizon according to Schlüter does not appear to have been represented in the Teutoburger Wald, unless his Gmuendense bed and the broken beds mentioned on page 48 of his work be considered the equivalent of all the beds between the Angulatus and Raricostatus horizons.

The English fauna, according to Wright's "Lias Ammonites" and the collections examined by me, has all the principal forms, and often very large shells, and there are also, as in the Côte d'Or and Rhone basins, representatives of the extreme modification of this genus, Ast. Collenoti.

This series had, therefore, a more general development in all the basins we have considered than any of the preceding series, but in spite of this there seems to be a preponderance of forms in favor of England and France. The unusual case of an early appearance of the radical species Ast. obtusum in the Luxemburg region should have its due weight, but the evidence of an equally early occurrence in the South German basin shows that Ast. obtusum probably made its appearance as an autochthone upon the level of the Upper Bucklandi bed in the South German basin, and was thence distributed. It is probable that the series subsequently met with more favorable conditions in the Côte d'Or and in England than in any other basin.

### OXYNOTICERAS.

Oxynoticeras oxynotum, the radical species of its peculiar series, appeared in such profusion and with such excessively compressed and involute whorls in the Northeastern Alps, South Germany, the Côte d'Or, and England, that one seems to be dealing with contemporary migrants from some unknown fauna. With regard to this conclusion, however, it may be well to be cautious. The morphological gap is not so great as appears between an adult of a species like Oxyn. oxynotum, and Agas. striaries or lavigatum. This is indicated clearly by the development of the individual in Ast. obtusum, oxynotum, and Agas. Scipionianum, as we have tried to show in the previous pages and in the descriptions of the genera and species. Oxyn. oxynotum was a species with a highly accelerated development, and in such forms the departure from allied forms took place suddenly. In consequence of this abbreviated mode of evolution gaps were left in the series which it is difficult to fill. The evidence with regard to the connection of Ast. Collenoti with Ast. obtusum and the young forms of Oxyn. oxynotum,

<sup>&</sup>lt;sup>1</sup> See young of Oxym. oxynotum, pl. x. fig. 4, 5, and 14-17, and Summ. Pl. xiii. fig. 9, 10, and compare with Agas. lævigatum, pl. viii. fig. 9, 10, and striaries, pl. ix. fig. 14, 15.

which convinced me of the derivation of that species from Agassiceras, was found in 1873 in the Stuttgardt collection. The specimens of the last named species had been selected by Professor Fra's out of several barrels of specimens of the same species gathered in the same locality. I looked very carefully in all other collections, handling hundreds of specimens, without finding any duplicates of these forms.

Hauer has given, in his "Nordöstlichen Alpen," an involute form, apparently the same as Oxyn. Lymense, and figures of the young, which are, however, in part distinct. His Amm. Greenoughii is evidently a member of the same subseries, and identical with the more involute forms of Amm. Guibalianus of Reynés. This subseries is only sparsely represented in the Northeastern Alps, and its date of appearance is not yet settled.

The collection at Semur has this species in the Birchii or Tuberculatus bed. M. Collenot states that this bed in the Côte d'Or basin contains the same species and is equivalent to the Tuberculatus, Obtusus, Oxynotus, and Raricostatus beds of South Germany and England, and that it is not possible to separate the faunas, as has been done elsewhere. The appearance of the usual forms of Oxyn. oxynotum in great abundance in Southeastern France according to Dumortier, and also of Oxyn. Simpsoni and Lymense, shows that the last named forms may have made their first appearance in France. This is further substantiated by the fact that Oxyn. Lymense, according to Wright, is found more abundantly in the South of England than in the midland counties. The appearance of Oxyn. oxynotum and Lymense in the basin of the Northeastern Alps can be accounted for by chorological migration, in the same way that we have accounted for the presence of Asteroceras and others in that basin. The radical species, oxynotum, is cited by Schlönbach 3 from only one locality in North Germany, and is not mentioned at all by Dr. Brauns in his "Unterer Jura nördwestlichen Deutschland," or by Emerson.

The second subseries of this genus is completely represented in the fauna of France. Three species only are found in England, none in South Germany, and two in the Northeastern Alps. Apparently none have been found in North Germany 4 or Luxemburg. The collections at Semur contain a nearly complete series of forms, and Dumortier has added others occurring in the Rhone basin. The home of the series, therefore, appears to have been in the Côte d'Or or Rhone basin.

This is the only series of the Arietidæ which overstepped the boundaries of the Lower Lias. Other species have been reported by various authors as occurring in the Middle Lias, especially the Jamesoni bed; but these were found asso-

<sup>1</sup> Denkschrift. Acad. Wien, XI., pl. xiii. fig. 6, 7.

<sup>&</sup>lt;sup>2</sup> Fig. 6, 7, appear to us to belong to some species of the second or Greenoughi subseries.

<sup>&</sup>lt;sup>3</sup> Eisenst, etc., Zeitsch. deutsch. geolog. Gesellsch., XV., 1863, p. 502. Amm. affinis, however, described in Paleontogr., XIII. p. 170, pl. xxviii. III. fig. 1, by the same author, is from Middle Lias, Greene, Brunswick, which is very similar to if not identical with Oxyn. oxynotum. We have not cited it in the table, however, since it may prove to be more nearly connected with Oxyn. Oppeli than with oxynotum.

<sup>&</sup>lt;sup>4</sup> Schlüter describes Oxyn. Oppeli of the Middle Lias as occurring at Altenkirchen and Borlinghausen in the Teutoburger Wald, and Schlönbach describes and figures the same from Amberg.

ciated with Cal. raricostatum, and therefore, according to our classification, are in the Lower Lias. Oxyn. Oppeli and numismale survived in the Middle Lias of Germany, Oxyn. Oppeli alone in the basin of the Rhone, and Oxyn. numismale alone, in England.

#### FAUNA OF SOUTH GERMANY. - TABLE I.

The notable facts brought out by this table are the following. The abundance and concentration of schlotheimian forms in the Angulatus zone, and their early appearance in the Rhætic. The completeness of the Caloceran series in the lower horizons, and the poverty of the faunas existing between the Geometricus or Upper Bucklandi beds and the Raricostatus bed in respect to these series, and also in the vermiceran, arnioceran, and coroniceran series. The asteroceran series reached a high stage of development as regards the number of forms, but is not represented by the extreme modifications noticeable in the basin of the Rhone. The oxynoticeran series is also present, and even passes into the Middle Lias, but has not a full representation of species.

## FAUNA OF THE CÔTE D'OR. - TABLE II.

The Ammonites at Semur were named by M. Reynés, and these names have come into circulation through publication by M. Collenot in his "Description Géologique de l'Auxois," and have also been quoted by Zittel and several other authors. Reynés considers many well-marked varieties to be distinct species. This is our principal disagreement with this author, and the following notes, together with the descriptions of species and table, sufficiently explain other differences of opinion.

Terquem's figures of Hettangensis <sup>1</sup> show a keeled, broad caloceran form with pilæ in the young, which belongs somewhere between Cal. laqueum and raricostatum. The specimens in the Museum at Semur, identified as Hettangensis by Reynés, do not agree with these figures. The specimens identified as Delmasi belong to several species, and one of these is so exactly like Pirondi, as figured by Reynés in his unpublished plates, that I have quoted this name as a synonym for Johnstoni in the table.

With regard to the vermiceran series, we traced the relations as follows. Beginning with spiratissimum, the forms appear to grade into Schlænbachi, which represents Conybeari in the Scipionis bed, then into rotator, which is a close ally, if not identical with Amm. caprotinus, D'Orb., and also with the spinous varieties of Conybeari found in Germany. The simpler ribbed forms grade into conybearoides, Rey., which is not very far removed from spiratissimum, thence into true Conybeari, and thence into Breoni, which last is a stouter and more robust form. Breoni, Rey., exactly agrees with typical Conybeari, and also with German forms of the same name, whereas Conybeari, Rey., is equal to our Bonnardi. Bochardi, Rey., has the form and characters of Conybeari during its earlier and adolescent stages, but

<sup>&</sup>lt;sup>1</sup> Pal. Lias. de Luxem., etc., Mém. Géol. Soc. France, V., pl. xiii. fig. 1, a, b.

has no tubercles. The specimens are large shells, and afford fine examples of the senile stages. *Debilitatus*, Rey., is similar to our lowest transitional forms of *Conybeari*. It may be a direct descendant of this from earlier times, or, more likely, a degenerate form. This grades into *Landrioti*, Rey. (D'Orb.), which is simply a more compressed form.

The occurrence of a form like Arn. falcaries in the Angulatus bed at Semur shows that we may anticipate in the future the finding of the radical arnioceran forms at this level or earlier. It is also very interesting to note that Arn. Hartmanni, of the Birchii or Tuberculatus bed, is a morphological equivalent of raricostatum, being, with the exception of the young, very similar to that species.

The more interesting facts shown by this table are as follows. The succession of the forms in the schlotheimian series has remarkable regularity, according very closely with their genetic relations. The caloceran series, though very complete in the lower beds, is not so fully represented as in South Germany. Higher up in the Birchii or Tuberculatus bed of Collenot, and probably upon the highest level at about the time the Raricostatus bed of other basins was being deposited, the series had an unusual number of forms. The vermiceran series has a most extraordinary display of varieties, but apparently not quite so full a representation in the lowest beds as in South Germany. Arnioceras is more fully represented in the Bucklandi beds than in any other fauna, and has also many species in the higher beds. The coroniceran series has a similar history, but is not more fully répresented than in South Germany. The agassiceran and asteroceran series are also very fully represented, and have the most highly modified species; the absence of Brooki will therefore probably be supplied at no distant day. The oxynoticeran series has also a complete history, and probably is nearer perfection than is shown in the table, but it nevertheless seems to have had no Middle Lias forms.

## FAUNA OF THE RHONE BASIN. - TABLE III.

The basin of the Rhone is equally important with that of Semur, and we give below a list of Dumortier's species and their synonyms in the different horizons. Dumortier mentions only *Burgundiæ*, and fragments of *Johnstoni* and *planorbis*, in what he calls the Planorbis bed. This indicates the possible absence of the lower beds of this horizon, since this is evidently the fauna of the Caloceras bed.

The Angulatus horizon has a fauna less rich in species than that of the Côte d'Or, especially when one considers the large number of localities from which the author's collections were gathered. The list includes, besides the species given in the table, *Amm. bisulcatus*, a very doubtful form. It may be a form of *Conybeari*, or similar to the peculiar sulcated form described in the note above on page 70, but it is probably not a true *Cor. bisulcatum*.

There are no transitional beds mentioned between this and the bucklandian horizon, and the beds are evidently not so fully presented, either geologically or paleontologically, as in the basin of the Côte d'Or. The list is very meagre as compared with that in the corresponding beds at Semur, but the presence of

Scipionianus indicates that the bucklandian horizon of this basin represents the Lower Bucklandi beds of other basins.

Dumortier divided his zone of Amm. oxynotus into four beds, distinguished by their faunas.

The "Davidsoni bed" should have been called Striaries bed, since his Amm. Davidsoni is identical with Agas. striaries. The list of species does not enable one to synchronize these beds with the Tuberculatus beds of Semur or other basins, nor do they show that it is equivalent to any bed above the Upper Bucklandi beds.

The Stellaris bed of Dumortier contains, besides the species mentioned in the table, Amm. Locardi, a species of Deroceras, and Amm. Birchi, a form of Microderoceras; both of these, therefore, belong to a family distinct from the Arietidæ. The presence of Birchi, Boucaultiana, and obtusum show that this, and not the so called Davidsoni bed, is the equivalent of the bed immediately above the Upper Bucklandi beds at Semur. This result confirms our opinion that the Davidsoni bed of Dumortier should be called the Upper Bucklandi bed.

Dumortier's Planicosta bed contains Cluniacensis,<sup>2</sup> which is identical with Ast. Collenoti; and this seems to settle the geological position of this important species. Amm. jejunus<sup>3</sup> seems to be an abnormal or diseased Arn. miserabile; Pellati is a young form of Cal. raricostatum; and armentalis,<sup>4</sup> if one can trust the aspect of the inner umbilical pilæ, is a diseased form of Cal. raricostatum. It appears from the figure to be similar to the deformed Amm. longidomus æger of Quenstedt,<sup>5</sup> and other similar pathological forms, in which the keel and channels have been superseded during growth by pilæ crossing the abdomen.

Viticola (Plate XXXI. Fig. 9-13) is the same as the Johnstonian variety of Cal. raricostatum; Edmundi (Plate XXXIX.) is the equivalent of the young of Cal. nodotianum; turdecrescens (Plate XXXI. Fig. 3, 4) may be related to Arn. falcaries. The umbilicus, sutures, and general aspect of the last indicate that it is a form of Arnioceras. Oosteri (Plate XXX. Fig. 2-4) is a keeled and channelled form of Arnioceras, with distorted pilæ.

Amm. planicosta, subplanicosta, and Pauli are all varieties of our Der. planicosta, and belong to a family distinct from the Arietidæ.

The three upper beds of Dumortier are apparently the equivalents of the Birchii or Tuberculatus beds in the table of the Côte d'Or basin.

The notable facts brought out by this table are as follows. There is a regularity in the distribution of the schlotheimian series similar to that in the Côte d'Or basin. Caloceras is not so fully represented in the lower beds, and is equally deficient in the Bucklandi zone. It is represented by a full list of species in the highest beds, with the exception of nodotianum, which is absent. Cal. carusense, however, is more fully represented, and Cal. raricostatum has a greater number of varieties than in any other fauna. The arnioceran series is not so fully represented in the Bucklandi zone, but it is notably richer in forms in the highest beds than in any other fauna. Coroniceras is well represented in the

8 Pl. xxxi. fig. 6-8.

<sup>&</sup>lt;sup>1</sup> Pl. xxi. fig. 1-4.

<sup>&</sup>lt;sup>2</sup> Pl. xxv. fig. 8-10.

<sup>&</sup>lt;sup>5</sup> Die Amm. d. Schwab. Jura, pl. vi. fig. 3.

lowest beds and in the Bucklandi zone, but is deficient above. Asteroceras is probably more fully represented than is shown in the table, since the extremes of the series have been found, and, the fauna being near to that of the Côte d'Or, there are grounds for anticipating the discovery of intermediate forms. Agassiceras is complete in its lower forms, but Scipionis has not yet been found. The oxynoticeran series is not only quite complete, but has also a middle lias representative. As regards Schlotheimia, Caloceras, Vermiceras, Arnioceras, and Asteroceras, this fauna impresses one as containing the most highly modified derivatives, and as being possibly a residual fauna representing an acme of chorological migration and varietal modification so far as these genera are concerned. Possibly Oxynoticeras will also have to be included in this category, and then the parallel with the English fauna north of what we have called the zone of the autochthones would be complete.

## FAUNA OF ENGLAND. - TABLE IV.

In this table the same regularity of succession is found in the schlotheimian series as in the Côte d'Or and Rhone basins. Caloceras is again deficient in the Bucklandi zone, as in the Rhone basin, but is quite fully represented and has an extraordinary new form in the Raricostatus bed, Cul. aplanatum. There is also a curious parallelism with the Rhone fauna in the arnioceran series, which, as in that basin, has the extraordinary form of Arn. Macdonelli of the Raricostatus bed. Besides the general absence of radical species, except of course the generally distributed psiloceran and caloceran radicals, there is in this fauna a very important fact to be noted, similar to that observed in the fauna of the Rhone. The extreme modifications in the highest formations are very generally present,—more so than in any other fauna. Thus, besides Cal. aplanatum and Arn. Macdonelli there are doubtful forms of Cor. bisulcatum in the Oxynotus zone. Ast. Collenoti, Ast. denotatum, and the extraordinary series of var. sagitlarius of Ast. obtusum, are also present. The Oxynotum subseries is complete, and the second or Guibalianus subseries alone is imperfectly represented.

The English fauna is therefore a residual fauna, not only because of the absence of radicals, but because it presents a chronological and biological acme in the evolution of the most highly modified and most recent forms of the different series, thus clearly indicating chronologically and biologically its more recent derivation by chorological migration from the older, though apparently contemporaneous, faunas of the autochthonous zone.

### FAUNA OF THE PROVINCE OF CENTRAL EUROPE. - TABLE V.

This table has already been amply explained, with the exception of certain general facts. The independent origin of the schlotheimian and psiloceran series is in strong contrast with the Northeastern Alps fauna, which as tabulated in Table VI. shows that Psiloceras and Schlotheimia are connected by means of intermediate wæhneroceran forms. Schlotheimia and Caloceras are character-

istic of the Planorbis zone; they were immediately succeeded in the Angulatus zone by a full presentation of schlotheimian, caloceran, and vermiceran species, that is, of the entire Plicatus Stock. This stock then entered upon a period of decadence, slight in the Lower Bucklandi, but more marked in the Upper Bucklandi bed. Arnioceras attained its greatest development in the Upper Bucklandi zone and was more persistent in the higher beds than Coroniceras. This last attained its fullest expansion earlier in the Lower Bucklandi beds, and declined rapidly in the Upper Bucklandi, and disappeared altogether in the Obtusus bed. This decline is shown by the geratologous characteristics of the species in the Upper Bucklandi beds, rather than by a less number of forms. Thus Cor. orbiculatum, Gmuendense, trigonatum, and the multicostatus variety of bisulcatum, are all degenerate species as compared with the forms of the Lower Bucklandi bed. They have more convergent-sided whorls, and these are usually developed at an earlier age.

Agassiceras also reached its acme in the Lower Bucklandi bed, but is more persistent, and has some forms in the higher formations. Asteroceras is the only series which attained its acme in the Obtusus zone, and then declined in the Oxynotus zone. The oxynoticeran series reached its maximum in the Oxynotus zone, and, though surviving the changes which attended migration into middle liassic habitats, became extinct in that formation.

The schlotheimian series is a highly modified series, composed of involute derivatives, and ceased to exist in the Obtusus bed, but there are a few dwarfed forms in the Oxynotus bed. Caloceras persisted in the highest beds, whereas its highly modified derivative series, Vermiceras, is shorter lived, and less fully represented in the highest beds. Arnioceras is parallel with Caloceras, and is the radical series from which the more highly modified and shorter lived Coroniceras originated. Agassiceras, the radical of the remaining series, persisted from the Angulatus to the Oxynotus bed, whereas the derivative Asteroceras and Oxynoticeras were both shorter lived. These series, even when thus minutely followed out, accord with the law of persistence in radical stocks, as expressed above, on page 26.1 Psiloceras itself is not persistent, and is an apparent exception. It is the last of a long line of paleozoic secondary radicals which survived in the Lower Lias. It can be compared with the upper part of a stem which has reached the point of growth at which it splits/ into many branches. Psiloceras was in like manner resolved into derivative forms, the arietian radicals Caloceras, Arnioceras, and Agassiceras.

We have already noted and discussed the rise and progress of each series: first, the radical stage, or epacme; second, the acme; third, the final decline, or paracme, caused by the prevalence of geratologous forms. The result of such a serial history, when the series are considered together as one family found within certain specified beds, is shown in this table. There is a precise parallelism between the history of the whole and of any one series. The Planorbis and

<sup>&</sup>lt;sup>1</sup> If, as we have inferred above, on page 24, the channelled and keeled species of Caloceras are transitional to *Hildoceras Walcoti* and other radical forms of the Carinifera, this opinion acquires additional strength, since Caloceras would then become the tertiary radical for the whole of the Carinifera of the Jura.

Angulatus zones contain principally radical species and their immediate derivatives. The Bucklandi zone is characterized, with some exceptions occurring only in the Upper Bucklandi bed, by the presence of truly progressive forms. The highest beds, the Obtusus and Oxynotus zones, are almost exclusively the homes of more or less degenerate and geratologous forms.

Extraordinary and unforeseen correlations, such as these, between chronological distribution and a biological classification founded upon the life history of the individual, cannot be accidental. We have already shown, in preceding chapters, that our classification of series is natural, and capable of verification by means of the cycles which are found to be present in the history of the individual and of the group. The process of verification does not, however, end with this, since approximately exact agreements may be found between the paleozoölogical and geological records wherever both classes of facts exist and have been minutely studied.

There is even some evidence that cycles may be traced in the so-called contemporaneous faunas of the same horizon. Thus, what we have said about the analdainic faunas of England and the basin of the Rhone indicates this possibility. These faunas show an extraordinary evolution of the geratologous forms of the geratologous series; the aldainic basins show, on the contrary, in so far as the Côte d'Or and South Germany are concerned, an extraordinary assemblage of the progressive forms of the Arietidæ, whereas the originating or aldainic centre of the family in the Northeastern Alps has a fauna in which the radical series are enormously developed. This would seem almost evidence enough that there are cycles in the chorological migration, as well as in the chronological evolution of forms. The whole might be represented as a complex of vortices, in which the result is apt to be a cycle, whether the spiral lines of evolution form small vortices upon the same or nearly the same horizons, or whether the picture is the blending of all these into one great spiral, or a series of more or less parallel and blended spirals ascending through geologic time.

#### FAUNA OF THE PROVINCE OF THE MEDITERRANEAN. - TABLE VI.

It was intended to omit this table, as well as those of the North German basin, Italy, Corsica, Spain, etc., the species of which have not yet been fully described and illustrated, since it is not practicable in such researches to accomplish much unless aided by very full information. Lists of names from which these faunas might have been made up are rarely of much use, since authors differ essentially in the identification of species, and therefore we have not considered it safe to venture upon tabulating them. The publication of Wähner's and Neumayr's researches, however, induced the author to attempt to give a tabular view of the Mediterranean province. It has not been found practicable to carry out the system of connecting the forms by lines representing genetic bonds, except in so far as they have been published by the authors named above, and the usual connecting lines have therefore been omitted in series occurring above the Lower Bucklandi bed, and in all the genera of the Levis Stock.

The mixed faunas of the Adneth and Hierlatz beds, and of the gray lias limestones and Fleckenmergel, have been described by Gümbel, by Dionys Stur,2 and by Geyer,3 with very interesting remarks upon the similar faunas elsewhere. The first author regards the faunas of the Adneth and Hierlatz limestones as having species representing not only the various faunas of the Lower Lias, but also the faunas of the Middle and even Upper Lias. Oppel considered the Hierlatz beds as the equivalent of the Obtusus, Oxynotus, and Raricostatus beds.4 Geyer, who has examined this locality in detail, thinks, if it is compared with any single fauna, that we should have to select that of the Oxynotus bed. He however calls attention to the occurrence of Ast, obtusum and Cal. raricostatum in the same horizon, thus demonstrating the mixed character of the fauna. Stur regards it as possible that the different beds of the Lower Lias may, by further investigation, be defined in the Adneth and Hierlatz beds. This conclusion, however, rests upon theoretical considerations, and not upon actual observations, and this author observes, "dass in den Alpen einzelne arten der Lias fauna höher oder tiefer hinauf und herabreichen als in den ausseralpinischen Schichten beobachtet wurde, . . . und . . . während der Liaszeit innerhalb der Alpengebiets eine weniger streng geschiedene und minder mannichfaltige Gliederung wirklich vorhanden ist." 5

Both Stur and Gümbel distinguish only three faunas in the Lower Lias of the Kammerkahr Alps: 1. A yellowish limestone with a species similar to Johnstoni. 2. An intensely red limestone with Amm. spiratissimus of Hauer, Liasicus of Hauer, Haueri, Kridion, Ceras, Bodleyi, Hierlatzicus, Grunowi, bisulcatus, oxynotus, euceras, Charmassei, acutiangulatus, Doetzkirchneri, Hermanni, Kammerkahrensis, Partschi, cylindricus, Lipoldi, Foetterli, Petersi, but in which, however, a true Bucklandi bed was not distinguishable according to Gümbel. 3. Above this, thinner layers with Amm. raricostatus, zithus, densinodus, and a form similar to stelluris. Gümbel states that the Adneth or dark red limestones, the Hierlatz, and the gray limestones of Gastatter Grabens are equivalent to one another, and that each contains a mixture of species from Lower, Middle, and Upper Lias.

Suess and Mojsisovics distinguish a Planorbis, an Angulatus, a Bucklandi, a Tuberculatus, and an Obtusus bed in the Osterhornes mountains, but consider the Angulatus bed as the equivalent of the Enzesfeld limestones, and the Obtusus bed as the equivalent of the Adneth limestones. The fauna found by them did not, however, so far as published, appear to justify this conclusion.

Wähner 7 gives a clear statement of the facts in his "Heteropischen Differenzirung des alpinen Lias." He quotes Stur 8 as having distinguished two beds at Enzesfeld, the yellow limestones of the Angulatus zone underlying the true red limestones of the Adneth or Rotiformis horizon. The various localities of the

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<sup>1</sup> Geogn. Beschreib. d. bayer. Alpen, pp. 428-432.
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<sup>&</sup>quot; Geol. d. Steirmark. <sup>3</sup> Ceph. Hierlatz-Schichten. <sup>4</sup> Neues Jahrb. 1862, p. 60. <sup>5</sup> Geol. d. Steirmark, p. 433. 6 Op. cit., p. 195.

<sup>7</sup> Verhandl. k. k. geol. Reichsans., p. 168.

<sup>8</sup> See Stur, Lias Hirt. u. Enzesf. Jahrb. geol. Reichs., 1851, pt. 3, pp. 19, 24.

Mediterranean province are summarized by Wähner in this very satisfactory paper, and one sees that the lowest beds are apt to be well defined, but that after passing through the Angulatus zone definition becomes more difficult, so that even this author, for whom as an acute discriminator of species we have a great respect, seems not to have been able to define the separate beds in either the Adneth or the Hierlatz limestones.

Herbich makes a valuable contribution to this problem in his Széklerland, in which he describes several species of the Arietidæ, including an Asteroceras like stellaris of Hauer, equivalent to our obtusum, var. stellare, and Ægoc. Althii, which appears to be a true Microceras allied to Micr. planicosta, together with a number of species of the Lytoceratidæ, all occurring in a bed not over three meters thick, and he denies that any distinct beds can be defined.¹ Geyer, in the work above quoted, gives a detailed argument for the probable admixture of faunas, and comes to the conclusion that Oppel's scheme of zones is not applicable to the Northeastern Alps so completely as it is to the formations of Central Europe. Favre, in his "Terrains Liassiques et Keuperiens de la Savoie," gives a list of localities in which mixtures of different faunas have been announced by various authors, and Geyer adds several other localities.

Favre considers that the species in such localities, among which he includes the Northeastern Alps, must have been protected from the geological changes which produced new forms and modifications in other localities, and adds that we must seek the causes of admixture in the continuation of sediments of the same nature, and in the configuration of the surface. His idea was, that the persistent species continued to exist in closed basins, where they were secure from the action of the causes that destroyed the faunas to which they originally belonged in other localities. This explanation has a reasonable sound, but it appears to us inadequate. We regard the species quoted as migrants from previously existing faunas, which, having found favorable homes in these localities, became the radicals of new series upon new horizons; or else they were survivors of the geratologous forms of faunas upon the same horizon, which, having found favorable conditions in these new localities, persisted perhaps somewhat longer than the parent series. We have not found adequate evidence of closed areas, except perhaps between the western extension of the Mediterranean province as a whole, and that of Central Europe. The basins of the Lower Lias were evidently not, as a rule, so completely closed as to keep out migrants from other basins and provinces, since all the evidence tends to prove the constancy and uninterrupted migration of species throughout the faunas of Central Europe and the Mediterranean province.

Whatever hypothesis is maintained, there seems to be no possible way of accounting for the finding of a species in a truly anachronic position; that is to say, in a bed which belongs to an earlier horizon than that in which it has been proved to have originated. A specimen of *Coroniceras Bucklandi* in the Planorbis bed, or even in the lower part of the Angulatus bed, would introduce great

confusion into any stratigraphical or genetic classification. We have not yet been able to find any such case.<sup>1</sup>

Examples of mixed faunas such as have been quoted above are not so extensively mixed as has been claimed. The Hierlatz and Adneth limestones are, for example, mixtures only of the faunas of the beds above the Angulatus bed; the examples given of so-called psiloceran forms as occurring in them are due to mistakes in identification, since these forms are species or young of species of Arnioceras or Agassiceras, and the species cited as belonging to the Middle and Upper Lias are either radical forms or else morphological equivalents, like all the so-called anachronic forms which we have yet studied. A paper by W. B. Clarke is very instructive in this connection, since he found in the Rhætic a true Arcestes, showing conclusively how favorable this region must have been for the preservation of ancient forms. He also was able to make out and describe the Planorbis and Angulatus horizons, with a full list of species already described by Wähner and others, and, above this, the Hierlatz horizon.

The facts appear also to accord perfectly with the theory of autochthonous faunas. If the Northeastern Alps were the seat of origin for the major portion of the radical forms of Arietidæ, we should naturally expect to find in this province the geological and zoölogical relations which are shown in Table VI.; namely, a clear definition of the lower formations and faunas throughout the Planorbis and Angulatus horizons, and an extraordinary number of radical species and their immediate allies, these also having in the sutures a more ancient or triassic aspect than in Central Europe. An analdainic fauna made up of modified forms arising by migration from other faunas would necessarily be shown either in the admixture of forms above these horizons in case the sediments were similar and continuous, or else in the non-appearance of new radical or progressive forms if the sediments were more varied and more distinctly separable, as in England and in the basin of the Rhone.

While the Mediterranean province was an analdainic fauna so far as the Arietidæ were concerned during the deposition of the upper beds of the Lower Lias, subsequent to the deposition of the Angulatus beds, this was by no means the case with other groups, such as the Lytoceratidæ. On the contrary, as has been already announced by Neumayr, this province was the autochthonous home of this family, and Neumayr's opinion is strongly sustained by the remarkable series of species described from the Northeastern Alps by Geyer, Hauer, and others, and an especially fine series by Herbich from Siebenburgen. The Lytoceratidæ are by no means absent from the faunas of the Lower Lias in Central Europe, though generally quoted as being found in the Middle and Upper Lias. Thus Amm. Driani, Dumortier, and Amm. Salisburgense and Amm. allus of the same author, are apparently members of this family, found in the Oxynotus bed of the basin of the

<sup>&</sup>lt;sup>1</sup> Barrande, with all his knowledge and close study of the fossil Cephalopoda, has not been able to prove a single example. Those he has given are readily explained as morphological equivalents, and we have found by the investigation of Bohemian specimens that the Nautili of the present time are entirely different from paleozoic forms. As soon as the næpionic and nealogic stages are studied and compared, they are found to be distinct. This is also true of his Gon. (our Celæceras) præmaturum.

<sup>&</sup>lt;sup>2</sup> Geol. Verhält. d. Geg. nordw. v. Achen-See.

Rhone. The last two are closely comparable in aspect with species figured by Hauer from the Adneth limestones.¹ In the same way, we should be disposed to regard the Mediterranean province as the autochthonous home of some genera of the Middle Lias, which appear here in association with the Arietidæ.

The Arietidæ afford an excellent standard, since their genera and species have been found, with rare exceptions, only in the Lower Lias; and, so far as our knowledge now goes, the series of forms and cycles have a very complete and satisfactory aspect, indicating a history of progress and decline within the limits of that group of strata in the faunas of Central Europe.

In the Mediterranean faunas, however, so far as known, only the rise of the group is recorded in the sediments and fossil remains, and its acme and decline are not clearly indicated. We have been accustomed to look upon the fauna of the Hierlatz beds as composed for the most part of degraded dwarfs, whose peculiarities or modifications were due to the unfavorable action of the surroundings upon migrants from other contemporaneous faunas of the Lower Lias. This seems to be the only theory which can account for the prevalent smaller size and more or less degraded aspect of many of the shells, when compared with their nearest allies in other locations.

#### SUMMARY.

The facts cited above, though far from complete, show that the series of the Radical and Plicatus Stocks, with the exception of the vermiceran series, were probably evolved in the Mediterranean province. The series of the Levis Stock had however a different history, since they probably arose in the basins of Central Europe. We therefore venture to differ in part from the eminent geologist and paleontologist Neumayr, who regards, if we properly understand his views, the Northeastern Alps as the aldainic home of the whole of the Arietidæ.

The sutures of all the Mediterranean forms of Psiloceras and Caloceras are, as figured by Wähner, more complicated, or, as we should say, more triassic than those commonly found in Central Europe; but we occasionally find a variety of Psil. planorbe, like that figured by Quenstedt 2 and by Wright, 3 in which there is a close approximation to the outlines common in the Mediterranean province. After having written the above, we were extremely gratified to find precisely the same results with regard to the relation of caliphyllum and planorbe, but more fully and exactly stated by Neumayr, in his "Unterster Lias" (p. 25). His conclusion, that planorbe is consequently a derivative of Psil. caliphyllum, and is characteristic of Central Europe, while the latter species is equally characteristic of the Mediterranean province, is sustained by the fact that the sutures of caliphyl-

<sup>&</sup>lt;sup>1</sup> The peculiarities of the senile whorls are similar to those of Oxynoticeras Lotharingum, and will lead to much confusion until the sutures and the young are fully known. It is quite possible that our own conclusion may be wrong in this respect, but the sutures of Salisburgensis and allus, Hauer, are Lytoceran, and the aspect of these compressed shells is very similar to that of those found in France, whose sutures are however unknown. The young are known only in Driani, which resembles some of the forms described by Herbich.

<sup>&</sup>lt;sup>2</sup> Amm. d. Schwab. Jura, pl. i. fig. 19.

<sup>&</sup>lt;sup>2</sup> Lias Amm., pl. xiv. fig. 1.

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tum become simpler with advancing age, and more like those of planorbe, and by the scarcity of the latter, which, though found by Wähner, is declared to be rare. One of Wähner's specimens was transitional to Hagenowi in its sutures, and this indicates that the province of the Northeastern Alps was the autochthonous home of caliphyllum, planorbe, and Hagenowi, and adds greatly to the probabilities in favor of Neumayr's hypothesis. In Cal. Liasicum, Johnstoni, and nodotianum it is common to find varieties varying in the sutures between the Mediterranean and Central European extremes of modification, the latter being of course the most numerous in their own province and rare in the Northeastern Alps. The sutures of Liasicum, tortilis, and nodotianus, when contrasted with Quenstedt's, Wright's, and our own figures, give a good idea of the extent of variation, which is quite as great as in Psil. planorbe, if not greater.

Undoubtedly these facts, and the nearer approximation in aspect and sutures of the Mediterranean forms of Psiloceras to Gymnites of the Trias, the genus we have always regarded as the probable ancestor of the former, are strongly in favor of Neumayr's opinion that the forms of the European province arose by chorological migration from the apparently more ancient fauna of the Mediterranean province. The richer evolution of triassic forms in the Mediterranean province, as described and illustrated by Mojsisovics, can also be brought forward in favor of this view. Nevertheless, it is not right to yield entirely to the fascinations of this opinion until there is positive proof that *Psil. planorbe* or *caliphyllum* occurred earlier in this province than in Central Europe.

With regard to the origin of Caloceras from this province, the facts are still stronger in favor of Neumayr's view, but Vermiceras appears to have arisen in South Germany.

With regard to the origin of Wæhneroceras and Schlotheimia, it seems probable from the zoölogical evidence that they also arose in the Mediterranean province. The evidence is, however, geologically incomplete, since it is probable that Schlot. catenata occurred quite as early in South Germany. Wæhneroceras, the series of connecting forms uniting Schlotheimia and Psiloceras in this same province, is not yet proved to be of as ancient origin as Schlotheimia itself, and this introduces an anachronism which requires additional facts for its explanation.

Mösch<sup>5</sup> has decided that the Lias to the west of the head-waters of the Rhine contains species peculiar to the Central European province. W. A. Ooster's descriptions and figures of species confirm this conclusion, since he does not mention any novel species, though he describes twenty-one forms, representing more or less all the genera of the Arietidæ.<sup>6</sup>

Zittel <sup>7</sup> remarks that there is great resemblance between the Upper Lias in Provence and Lombardy. Mojsisovics, in quoting these observations, says that

<sup>&</sup>lt;sup>1</sup> Verh. k. k. geol. Reichsans., 1886, p. 169.

<sup>&</sup>lt;sup>2</sup> D'Orb., Terr. Jurass., I. pl. xlviii. <sup>3</sup> Ibid., pl. xlix. <sup>4</sup> Ibid., pl. xlviii.

<sup>&</sup>lt;sup>5</sup> D. Jura Alpen d. Ost-Schweiz, 1872, p. 1.

<sup>&</sup>lt;sup>6</sup> Cat. des Ceph. des Alpes Suisses, Denk. schweiz. Gesellsch. Naturwis., XVIII., 1861; see also Studer, Geol. d. Schweiz, II. p. 231, for similar views.

<sup>7</sup> Central-Appenn., Geogn. pal. Beitr., Beneke, II. p. 174.

<sup>8</sup> Dolomit Riffe Süd-Tyr. und Venet., p. 26.

they raise the question whether the Mediterranean forms of the Swiss Alpine Jura may not have come by the way of southern France into the western Alpine region.

The very interesting and instructive essay of M. Dieulefait on the "Zone à Avicula contorta et l'Infra Lias dans le Sud-est de la France" shows that in Provence a southern and northern basin may be clearly separated. The southern or Mediterranean basin comprises a range of deposits reaching from the neighborhood of Toulon and Brignolles to Draguignan, Grasse, and Nice. The basin of the north and northwest, or of the Durance, encloses the valley of that river and the neighborhood of Castellane and Digne in the department of Basses Alpes. The basin of the Mediterranean possesses a series of beds identified as belonging to the zone of Avicula contorta, but there are no Ammonitine, and all the beds above these in the Lower Lias are absent. In the basin of the Durance, however, a very complete series of lower lias beds, including a Planorbis and Angulatus bed, has been described. M. Dieulefait has here traced the limits of the Mediterranean province at a very important, and for our theory an essential locality. He has shown that the sharp division between the Mediterranean faunas and those of Central Europe, which, according to our conclusions, ought to exist along the boundaries between the basin of Italy and of the Rhone, can be actually traced in the field.

Dumortier's extensive observations in the valley of the Rhone and Collenot's at Semur show the sudden spreading out by migration of forms of Psiloceras and Schlotheimia from South Germany into the Côte d'Or at about the same time, and a somewhat later appearance of these radicals in the Rhone and North German basins, and possibly still later in England. It seems more likely also, from the two tables given above, that the species of Schlotheimia, Psiloceras, Caloceras, and perhaps Vermiceras, were migrants from the Côte d'Or basin to the Rhone, than that the reverse should have taken place. Coroniceras also thins out in this direction, whereas the genera having their acme in the upper horizons of the Lower Lias, viz. Asteroceras, Agassiceras, and Oxynoticeras, are more abundantly represented, perhaps, than in the Côte d'Or. All the information obtainable with regard to the faunas of the Lower Lias in Switzerland indicates a general thinning out in numbers of species and varieties in that basin which, like the basin of the Rhone, lies to the south of the autochthonous zone.

Emerson's collection from Markoldendorf now at Amherst, Mass., and others we have seen, show that the fauna of North Germany was probably derived from South Germany, and this accords with Seebach's conclusion, that a connection existed between the Hanoverian and South German faunas during the time of the deposition of the Lower Jura.<sup>2</sup> There is considerable doubt whether the English species of Psiloceras and Caloceras came by the way of the Côte d'Or, or found this locality by independent migration. The former opinion is supported by the general fact that the English fauna does not contain an autochthonous series, nor does any radical species appear earlier in this basin than in those of the continent; it is therefore probably a residual fauna, peopled by chorological migration.

<sup>&</sup>lt;sup>1</sup> Ann. des Sci. Géol., I. 1869, p. 473, pl. v.

<sup>&</sup>lt;sup>2</sup> Hannoverische Jura, p. 70.

The prevalence of the geratologous forms of the different series in the highest beds of the Lower Lias indicates that this fauna, like those of the Swiss and Rhone basins, is also a residual fauna, but lying north instead of south of the zone of the autochthones. The only definite information with regard to the Lias faunas of the higher northern latitudes, which I have been able to lay hands on, is the "I Sueriges Aldre Mesozoische Bildungen," by B. Lundgren.\(^1\) Cor. Bucklandi and bisulcatum are mentioned, and Cor. Sauzeanum,\(^2\) Agas. Scipionianum,\(^3\) Agas. striaries,\(^4\) and Arn. falcaries are figured.\(^5\) These indicate the presence of the Bucklandi beds in northwestern Sweden, but the fossils were in bad condition and not abundant in the number of species. Lundgren mentions, also, that these beds are underlaid by an unfossiliferous bed, which he thinks is probably the equivalent of the Planorbis and Angulatus beds of Central Europe. M. Hebert has, in his interesting paper, "L'Age des Grès à Combustible d'Helsinborg et d'Hoganas,"\(^6\) given proofs of the presence of the existence of the Planorbis and Angulatus beds in southern Sweden, but they contain no specimens of Ammonitinæ.

It is well known that the Lias does not exist in Central Russia, and A. Pavlow, in his article on "Russie, Esquisse Gologique," gives an account of the deposits of the Jurassic, but mentions the Lias as occurring only in the Crimea and perhaps the Caucasus, and refers these to the fauna of the Mediterranean province, and not to Central Europe. Savi E. G. Meneghini, "Geologia della Toscana," gives several lists of fossils from many distinct localities, among which are a number of the Arietidæ. Von Rath<sup>8</sup> quotes a list of fossils from Meneghini containing many Arietidæ, and he states that there are a number of new forms; but lists of names and descriptions of species are unfortunately not usually of value in such work as we are striving to do. Taramelli, in his monograph, "Del Lias nelle Provincie Venete," describes and figures several species of Ammonitine. His Amm. Guibalianus is a true Oxyn. Guibali of considerable size, 300 mm. in diameter, and too involute for a specimen of Greenoughi, rotiformis is a young form of Cor. Gnuendense, or some such compressed shell; it is assuredly not rotiformis if his figure is correct. Ar. obtusus is a true obtusum. Ar. stellaris is the adolescent form of Ast. stellare. All of these have the facies of the Northeastern Alps, except perhaps Guibali, which is new to us as occurring in the Mediterranean province.

Sacco states, in his "Lias della Valle Sturio di Cuneo," 10 that all the beds of the Lower Lias are present, and gives lists of fossils, including a supposed Psil. planorbe, several species of Schlotheimia, Ver. Conybeari, and a doubtful Cor. kridion, and Cor. Bucklundi and bisulculum are said to be of good size and abundant near Pouriac. In "Lias Inferiore ad Arieti," by C. de Stefani, it is distinctly stated, according to Geyer, that the Lower Lias of Italy is divisible into only two parts; one which is similar to the Angulatus horizon, and yet contains the fauna of

Sueriges Geologiska Undersökning, ch. xlvii., Mollusk.
 Pl. iii. fig. 5-7.
 Pl. iii. fig. 9.
 Pl. ii. fig. 8.

<sup>&</sup>lt;sup>a</sup> Ann. Sci. Géol., I., 1869. <sup>b</sup> Annu. Géol. Universel, II., 1886, p. 302.

<sup>&</sup>quot; "Geogn.-mineralo. Fragm. a. Italien," Zeitsch. deutsch. geol. Gesellsch., XX., 1868, p. 320.

Atti dell' Instituto Veneto, ser. 5, V., 1880, Appendix.
 Boll. del R. Comitato Geol. d' Italia, XVII., 1886, p. 15.

Spezia, and another higher horizon, which is supposed to be the equivalent of the Bucklandi horizon. This last is said to contain Cephalopods representing all the later faunas of the Lower Lias, and some species are quoted as being referable to the Middle Lias.

Canavari, in his "Fauna der unteren Lias von Spezia," so frequently quoted above, states that the fossils occur in a single zone, which does not admit of subdivision, though it was carefully investigated, layer by layer, by Cocchi. He states also, that it is unquestionably the lowest of the lower lias sediments in Italy, and comprises all the horizons except those of Planorbis and Oxynotus. He considers that the fossils have closer affinities with those of the Mediterranean province than with those of Central Europe, a fact which seems to be established. The species of the Lytoceratidæ and of Amaltheus, etc., which are supposed to be anachronic and to indicate a fauna derived from the Middle and Upper Lias, appear to us to be found in their appropriate positions, like those of the Northeastern Alps. They may be either the radicals of the similar forms which occur in the Middle and Upper Lias of the Central European faunas, or morphological equivalents, or pathological specimens. This is also Canavari's opinion with relation to some forms, since he expressly states that the ægoceran species, as he calls them, are the immediate forerunners of Microderoceras. The fauna of the Rhone basin is almost exclusively composed of species having a Central European aspect. There are, it is true, some slight indications, in the presence of three species of Lytoceratidæ in this basin, that the migrants may have come this way on their march into-Central Europe, but there are no supporting facts with which we are acquainted. The absence of the Planorbis horizon, or at any rate its sporadic appearance in Italy, and the absence of Ammonitinæ in this horizon of southern Provence, are very serious difficulties in the path of a supposed southern track of migration.

The evidence, so far as known, seems therefore strongly in favor of the view, that during the time of Planorbis and Caloceras, and perhaps earlier in the Angulatus horizons, the stream of migration flowed south and westerly from the Northeastern Alps into Italy, while another from the same basin directed itself westerly along the then existing coast lines into the basins of South Germany and the Côte d'Or, and the species were distributed thence into the basins to the north and south of these two, in the province of Central Europe. In South Germany and the Côte d'Or the conditions became favorable during the time of the Angulatus horizon for the evolution of Vermiceras among the descendants of the Plicatus Stock, and for the origin of Coroniceras, Arnioceras, and Agassiceras of the Levis Stock. Asteroceras arose later in these same faunas in the Upper Bucklandi beds, and Oxynoticeras probably even still later, though here the series is evidently older than the date of its first appearance. The migrations of these genera spread the forms to the east into the faunas of the Northeastern

<sup>&</sup>lt;sup>1</sup> The figures of Amaltheus given by Canavari in his last work, "Fauna del Lias inf. della Spezia, R. Comit. Geol. d'Italia," III., Pt. II. pl. vi., are certainly startlingly similar to Amaltheus, but such resemblances in forms of widely distinct series are not uncommon. See the pathological case figured on Plate X. Fig. 19 of this memoir, and others quoted in the descriptions of the species.

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Alps, and thence they passed southerly into the Italian basin. Migrants also passed in all other directions into the residual basins to the north and south of the basins of the Côte d'Or and South Germany, in the province of Central Europe.

While these faunas in the Northeastern Alps and Italy became analdainic faunas so far as the Arietidæ were concerned, they were aldainic faunas for some other groups, like the Lytoceratidæ, and also very likely for the Liparoceratidæ, Deroceratidæ, and possibly other families. These mixed faunas, which have been deemed such sources of confusion, are in reality the most instructive, and will enable us to trace both chronological and chorological migrations with greater security, if the views here advanced are correct.

Table V. shows that there are but two examples of what Neumayr calls cryptogenous types in Central Europe, species appearing suddenly without apparent ancestors, Schlot. catenata and Psil. planorbe, var. leve. Schlot. catenata, however, cannot be called an unquestionable cryptogenous form in the Northeastern Alps. It is in that basin connected by intermediate forms, as stated above, with Psiloceras, and it is therefore probable that in course of time the geological evidences which are now confusing will be brought into accord with the paleozoology. Psil. planorbe is a radical derived from Psil. caliphyllum, or else from pre-existing triassic ancestors, and the absence of a complete series connecting it or Psil. caliphyllum with Gymnites of the Trias is evidently due to the absence of an equally complete series of formations. That the intermediate species might have been deep-sea forms, and therefore not represented in the rocky strata now exposed, as supposed by Neumayr, is an admissible explanation. Newberry's hypothesis 1 of the retirement of the sea is, however, equally supposable, and has the additional recommendation of explaining the absence both of intermediate forms and of the sediments. Newberry thinks that the presence of intermediate links in paleozoölogic history, and their absence from localities so far explored, are explicable on the supposition that the chain of the rocky deposits is incomplete in those localities, and that the sea had retired from them carrying with it the threads of life. The missing links of the record were then evolved in other places, but not brought back by the return of the ocean to its former shores. This seems to us more in accord with what is already known of the merely fragmentary aspect of the geologic record in any one region, the occasional discovery of the absent leaves of the record in other places, and the want of absolute synchronism between the strata of Europe and those of America.

That *Psil. planorbe* was a littoral form, as well as its congeners, can hardly be doubtful, since, besides the facts quoted above, they are found associated in the same series of layers with bones of saurians and even remains of insects in England. The remarks of Martin and other authors, quoted above, upon the characteristics of the lumachelle in the Côte d'Or, and the broken aspect of the shells of Ammonoids compared with those of swimmers like the Nautiloids, as stated by Terquem, in the department of Moselle, the opinions of Tate and Blake, and

<sup>&</sup>lt;sup>1</sup> Circles of Deposition in American Sedementary Rocks, Proc. Am. Ass. Adv. Sci., XXII., 1873, pp. 185, 189.

the great abundance in which Ammonoids occur as contrasted with Nautiloids, are all in favor of the conclusion that they were structurally rostrated, creeping animals, which necessarily followed the shore lines in their migrations. Fraas takes the view that the Suabian Lower Lias was as a whole, when compared with the synchronous strata to the west and north, a deep-sea formation, and cites the absence of sandstones and coarse deposits, the small Lamellibranchs, and Brachiopoda. It is very evident, however, that whatever the bathymetrical differences of the South German basin, and however far removed from the ancient shores now represented by the Black Forest and the Vosges, the surroundings were not sufficiently distinct to make any marked differences in the Arietidæ of this basin.

We have noted above the occurrence in Peru of Cal. Ortoni, a form having close resemblance to a species of the Northeastern Alps, and the apparent identity of other species with those of Central Europe, the forms found at Vancouver's Island and in California, etc., show that on this continent the faunas possessed a mixed character. The paucity of the development both geologically and paleontologically of the Lower Lias is in accord with the similar deficiency of this stage in the analdainic basins of northern Europe, India, and Italy. There is another fact in this connection, which strikes us as very remarkable, — the absence of any absolutely new types of Ammonitinæ. So far as explorations have gone, not a single species indicates the evolution of any widely distinct family or genus from those found in Europe. Thus, although not able to produce any satisfactory evidence that all the faunas throughout the world during the lower lias age were more or less analdainic faunas derived from the zone of the autochthones of the Arietidæ in Europe, the evidence is sufficient to make such an opinion worthy of the attention of students of geology and paleontology.

The view expressed by Neumayr, that the Cephalopoda are exceptional in respect to the rapidity with which their modifications probably took place, seems to us erroneous. There is no greater aspect of pliability in this than in other types, when accurately classified. When, however, we assemble within the same family species of the Lytoceratinæ and Ammonitinæ, or in the same genus forms of entirely distinct stocks without sufficient reference to their genetic history, then of course a belief in the polygenesis of the progressive series, and in an exceptional tendency to modification, becomes essential in order to explain the heterogeneous aspect of the groups. We think, however, that even the most variable families of Cephalopoda are not, as a rule, any more variable than the Unionidæ, Ostreadæ, or Hippuritidæ, among Lamellibranchs, or the Planorbidæ, Vermetidæ, etc., among Gasteropoda, and many other groups that might be mentioned.

The expansion of the whole series of forms of Psiloceras, Schlotheimia, and Wæhneroceras in the Northeastern Alps, and the apparent rapidity of chorological migrations and changes and introduction of new series, the equally sudden

¹ We desire to call attention here to the fact that we have admitted the polygenetic derivation of retrogressive types like Baculites, etc.; but this in no manner commits us to the doctrine of polygenesis for any of the progressive types. So far as we know, these are monogenetic in mode of origin.

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expansion of the Arietidæ in the Bucklandi zone of Central Europe, the rapidity with which the forms of the still later beds must have come into being in order to be presented in a body, as in the Tuberculatus beds of the Côte d'Or, and the limited thickness of the beds, are all against the supposition that it required vast periods of time for a species to become modified and give rise to series of distinct forms. Either the species of the Arietidæ had time enough during the deposition of the Planorbis, Angulatus, and Bucklandi beds of the Lower Lias to spread themselves over the entire area of modern Europe, and generate from one form all the series described above, or else the same species and genera had invariably distinct centres of origin in the different basins. One might support the latter view and favor polygenesis even in this extreme sense with considerable show of reason, if there were not such a mass of evidence in favor of migration, some of which we have given above. If there were space, we could add examples from the researches of various well known zoölogists upon the migrations and modification of species in modern times, both along the coasts and over the land. The more striking examples are, however, quite well known, and hardly need to be dwelt upon.

V.

## DESCRIPTIONS OF GENERA AND SPECIES OF ARIETIDÆ.1

## RADICAL STOCK.

FIRST, OR PSILOCERAN BRANCH.

#### PSILOCERAS.

SHELL smooth, plicated or with fold-like pilæ in some subseries. The abdomen is rounded, or with smooth median zone, never channelled or keeled. Whorl in section is compressed, helmet-shaped. The sutures are similar in proportions and outlines to those of Caloceras. This is shown in the broad abdominal lobe and large siphonal saddle, the equality in length and size of the abdominal and lateral lobes and saddles, their leaf-shaped marginal digitations, and the number and inclination posteriorly of the auxiliary lobes and saddles.

The living chamber is one, or more than one, volution in length, and is shorter in the young than in the adult stages.2 Senility is indicated by increasing convergence of the sides, and the loss of plications,3 but a subacute abdomen, such as appears in the old whorl of Wæhneroceras, is never present. The completeness and accuracy of Wähner's illustrations and descriptions, which enable one to study all the stages of growth in some species, has tempted us to suggest the existence of three subseries in this genus. (1.) The first contains smooth shells, typical helmet-shaped whorl, and an old age in which a subacute whorl is not yet recorded in any species. (2.) The second contains plicated shells exactly similar in form, but the folds numerous and regular, and in some species figured by Wähner these cross the abdomen with a forward bend. They are, however, not true pilæ, and, so far as we know, they do not become depressed along the median zone as in Wæhneroceras, (3.) The third contains shells having psiloceran forms but flattened sides, and often plicated as in the second subseries, though the Psil. Hagenowii is smooth. We regard this subseries as of doubtful utility, but do not know how to dispose at present of the forms it contains.

<sup>&</sup>lt;sup>1</sup> Throughout this chapter there is no attempt to give a complete synonymy of any one species. The references given under each name are only those which were considered essential to settle the application of the specific name and the range of the forms to which it was applied in this memoir. The localities given are those of specimens in the collections of the Museum of Comparative Zoology.

<sup>&</sup>lt;sup>2</sup> Quenstedt, Amm. Schwab. Jura, pl. i. fig. 6, shows a nealogic stage in which this chamber is not quite half a volution in length. Wähner takes note of this, (Unter. Lias d. nordöst. Alpen, Mojsis. et Neum., Beitr., IV., 1886, p. 135.) and states that in one example of Psil. planorbe from Würtemburg observed by him the living chamber was only two thirds of a volution in length, and suggests the same opinion with regard to the shorter living chambers of the young.

<sup>&</sup>lt;sup>3</sup> Quenstedt figures what may be a fragment of an old specimen of Psil. planorbe, Amm. Schwab. Jura, pl. iii. fig. 1, and Wähner has figured several old specimens in Unter. Lias, Mojsis. et Neum., Beitr.

FIRST AND SECOND SUBSERIES.

### Psiloceras planorbe, HYATT.

#### VAR. leve.

Plate I. Fig. 1-4. Summ. Pl. XI. Fig. 1; Pl. XII. Fig. 1.

Amm. planorbis, Sow., Min. Conch., V. p. 69, pl. cecexlviii.
Ægoc. planorbis, Wright, Lias Amm., p. 308, pl. xiv. fig. 1-4.
Amm. psilonotus levis, Quenst., Die Ceph., p. 73, pl. iii. fig. 13; Amm. Schwab. Jura, pl. i. fig. 1-7.
Amm. Sampsoni, Portl., Rep. Geol. Londonderry, etc., p. 138, pl. xxix. A, fig. 13.
Psil. planorbe, Нуатт, Bull. Mus. Comp. Zoöl., I. No. 5, p. 73.

Localities. — Whitby, Watchet, Montloy, Semur, Rudern, Nellingen, Balingen, Neuffen.<sup>1</sup>

This remarkable form is a somewhat flattened discoidal and perfectly smooth shell in its typical adult form. The young are often plicated.

#### VAR. plicatum.

Plate I. Fig. 5, 6. Summ. Pl. XI. Fig. 2.

Amm. psilonotus plicatus, Quenst., Amm. Schwab. Jura, pl. i. fig. 1-14 (not fig. 8, 13).

This shell differs from variety leve merely in having immature pilæ or folds in the neologic and ephebolic stages. There is therefore the most gradual and hardly perceptible gradation from the preceding variety to this form. The septa of both are exceedingly variable. The marginal digitations may be either very shallow, as in the Arietidæ generally, or they may be foliaceous and complicated, as in the radical series. The lobes and saddles may also vary exceedingly in size and proportions; some species have deep and narrow saddles with long broad lobes, as in the radical series, while others, more like the typical Arietidæ, have shallower, broader saddles, and shorter, more pointed lobes. In the collection at Semur there are forms from Saulieu identical with the South German, which when compared with raricostatum and Johnstoni, show closer approximations than any specimens seen elsewhere.

The Bristol collection contains undistorted specimens of this species from Cotham, and in Dr. Wright's collection from Whitby the plicatus variety is labelled Anm. erugatus, Bean. The connection with the flattened Watchet specimens of planorbis, Sow., can be clearly made out by the large tablet in the British Museum, containing about one hundred and fifty specimens. Of these, perhaps ninety exhibit folds like those of plicatus and erugatus. The largest on this slab is from 60 to 80.5 mm. in diameter. These large specimens are not equivalent to Cal. Johnstoni, as Oppel supposed, but to plicatus. Erugatus seems to be a dwarfed form with the folds often developed very strongly in the young, and the shell has fine strize of growth, as in Agas. striaries, Plate IX. Fig. 14, 15. In the Museum of Comparative Zoölogy the series is complete from leve to var. plicatum, as figured by Quenstedt in "Der Jura," and in another direction to the var. of planorbe from Semur. This is a slightly plicated form, having the sides of the whorls broader

<sup>&</sup>lt;sup>1</sup> These localities also include var. plicatum.

<sup>8</sup> See Pl. i. fig. 5, 6.

 $<sup>^2</sup>$  Amm. erugatus Bean has only the young plicated, resembling in this respect var. leve. It is however always a small form or dwarf.

than usual, and the involution slightly increased, a modification which is also sometimes present, though less marked, in *erugalus*.

Wähner found what he claims to be *Psil. planorbe* at Pfonsjoch in the Planorbis bed. These were small specimens, measuring 15-40 mm. in diameter, and one of them is said to be similar to Hagenowi. In the same work he figures the following discoidal shells of the smooth subseries: *Psil. polycyclum* and *caliphyllum*, Plate XV., and *Psil. pleurolissum*. Neumayr, in the Unterster Lias, gives *Psil. planorboides*, a more involute, smooth species of this series. *Planorboides* appears to lead into two much more involute and compressed species figured by Wähner in the same work, *Psil. Atanatense* and *mesogenos.* Both of these are devoid of true pilæ, and possess only senile fold-like pilations.

#### SECOND SUBSERIES.

### Psiloceras longipontinum, Wähner.

Amm. longipontinus, Opp., Pal. Mittheil., p. 129, pl. xli.

Psil. longipontinus, Wähner, Unt. Lias, Mojsis. et. Neum., Beitr., IV. p. 196.

"Egoc. Clausi, Neum., Unterst. Lias, Abh. k. k. geol. Reichsans., VII. pl. iii.

The original of this species in the Museum of Stuttgardt has considerable likeness to Psil. planorbe, var. plicatum. Oppel seems to have considered it one of the schlotheimian series.<sup>6</sup> The open umbilicus, straight folds in place of true pilæ, keelless abdomen, and helmet-shaped form of whorl, show it to be a member of the psiloceran series. The sutures,<sup>7</sup> as figured by Oppel, exhibit the strong psiloceran affinities of the species. In his specimen the last whorl has become smooth on one side, and the pilæ nearly obsolete on the other, thus indicating the approach of senility, though the shell is but 95 mm. in diameter. The pilæ begin to obsolesce posterior to the last septum. The living chamber is nearly one volution in length, though still incomplete. An empty cast in the Semur Museum from Ruffy undoubtedly belongs to this species; it is 155 mm. in diameter, and the last whorl is smooth, showing its great age. There are specimens in the collection at Munich labelled Amn. Roberti, Hauer, locality Filder, and Amn. Oeduensis,

- <sup>1</sup> Unter. Lias, Mojsis. et Neum., Beitr., IV. p. 136.
- <sup>2</sup> Ibid., III. pl. xxvi.

<sup>3</sup> Abhandl, geol. Reichsans., VII. pl. iv.

- 4 Op. cit., III. pl. xxvi.
- <sup>5</sup> We have figured only the most involute of this smooth series on Summ. Pl. xi. fig. 13.
- <sup>6</sup> The closeness of the parallellism between some of the forms of Psiloceras and some species of the Lytoceratidæ is such as will be likely to cause considerable confusion unless great care is taken in studying the species. Comparison of such forms as Amm. Petersi, Hauer, Ceph. nordost. Alpen, pl. xxi. fig. 1-3, Lyt. Petersi, Herb., Széklerland, pl. xx., Lyt.? Driani, sp. Dumort., Études Pal. du Basin du Rhone, and Lytoc. (Amm.) Roberti, Hauer, Capric. oesterr. Alpen, pl. iii., will show that without close study of the sutures and young no separation can be made with certainty. In fact, in identifying Driani in the absence of figures of the sutures as a form of Lytoceras, we have been led by the geological position and size, which accord better with Lytoceras than with a species of Psiloceras. It is possible that in doing this we are illustrating these remarks in a forcible manner.

See also in this connection the forms of Rhacophyllites and Phylloceras figured by Canavari in his "Fauna des unteren Lias von Spezia," pl. ii.

7 The sutures figured by Portlock, as well as the form of the section (b) of his Amn. Sampsoni (fig. 13 c, not fig. 13 a), suggest longipontinus, and may indicate the presence of this form or transitional varieties, in the English basin.

Despl. d. Champ., locality Blumenstein am Thuner See. One of the specimens from Filder shows the exact aspect and markings of *Psil. planorbe*, but has the form of *longipontinum*. Though it is somewhat difficult to judge from a figure, nevertheless, Æg. Clausi, Neumayr, very closely resembles *Psil. longipontinum*, and we have considered it to be a variety of this species with somewhat stouter whorls than the normal form. It is also a large aged specimen, and according to Neumayr came from Würtemburg.

Quenstedt referred this species, in his "Ammoniten des Schwäbischen Jura," to Cal. laqueum. His comparisons were evidently made with the old whorl of laqueum, and, as this has no keel, and is smooth or with obsolescent pilæ, it is of course very like the adult stages of Psil. longipontinum. Nevertheless, both the young and adult stages of laqueum are easily distinguished from the same stages of longipontinum. Quenstedt's figure shows the length of the living chamber to have exceeded one volution.

Tate and Blake's citation of this species from the Angulatus bed <sup>1</sup> is likely to mislead. Their species is, as figured, a diseased Caloceras, or poorly drawn species of Schlotheimia with pilæ crossing the abdomen, but certainly not, as named by them, *longipontinus*.

Species of the second subseries figured by Neumayr in the work quoted above are as follows. Psil. cryptogonium, Plate VI., is discoidal. Psil. majus and Gernense, Plate V., are slightly more involute shells. Wähner, in Volume IV. of the work above quoted, figures Psil. sublaqueum, Plates XV., XVI., Psil. crebricinctum, Plates XVI., XVIII., Psil. pachydiscus and polyphyllum, Plate XVII., all discoidal shells. This subseries and the preceding agree closely with the western European forms except in the involute species. Wähner also figures, in Volume III. of the same work, Psil. Berchta and aphanoptychum, Plate XXIII., which are discoidal, and Psil. pleuronotum, Plate XXV., calcimontanum, Plate XXIV., and Kammerkarense, Plates XXIV., XXV., which are more involute and compressed.<sup>2</sup>

# THIRD SUBSERIES.

# Psiloceras Hagenowi, Wähner.

Amm. Hagenowi, Dunk., Paleontogr., I. pl. xiii. fig. 22, pl. xvii. fig. 2.

Amm. Hagenowi. Terq. et Piet., Lias Inf. de l'Est de la France, Mém. Soc. Géol., VIII. pl. i. fig. 3, 4.

Amm. Hagenowi, Quenst., Amm. Schwab. Jura, pl. i. fig. 18.

Psil. Hagenowi, Wähner, Unt. Lias, Mojsis. et Neum., Beitr., IV. p. 196.

The form of this shell approximates to that of *Psil. planorbe*, var. *leve*, but the sutures are more widely distinct, and degenerate in outline. In Terquem and Piette's figure they resemble quite closely the sutures of *Popanoceras Kingianum* and *antiquum*, Goniatitinæ of the Dyas. The lobes of that figured by Quenstedt are not so coarsely dentate, and approximate more closely to the sutures of *Psil*.

<sup>1</sup> Yorkshire Lias, p. 273, pl. v. fig. 4.

<sup>&</sup>lt;sup>2</sup> On Summary Pl. xi., outline figures have been given of the principal forms, aphanoptychum, fig. 11, and Kammerkarense, fig. 12.

planorbe. The saddles sometimes have entire margins, as in some Ceratitinæ of the Trias. Neumayr's Hagenowi, in his "Unterster Lias Nördalpen," is not a true Hagenowi, if the sutures are correctly drawn. Such facts and the remark of Wähner quoted above (page 113) show that Hagenowi is probably a dwarfed deformation of Psil. planorbe, which is likely to occur in any locality, and has an independent existence as a race or species only in certain basins where it is abundant. It seems to indicate, wherever it appears, that Psil. planorbe has there been subject to unfavorable conditions.

Neumayr in the work above quoted, Plate IV. Fig. 1, gives a Psil. (Ægoc.) Naumanni, a good-sized species with numerous folds, compressed slightly convergent sides, and a rounded smooth abdomen, exactly the form and characters of his Hagenowi, except that it is more decidedly plicated. The smaller Psil. (Ægoc.) crebrispirale, Ibid., Plate V. Fig. 4, is probably the young of this shell. The sutures have complicated margins, as in other shells of this province, and are not similar to those of Hagenowi. We place it here until its exact affinities can be settled by the study of a series, or of the young.

Ægoceras Struckmanni,<sup>2</sup> Ibid., Plate VI. Fig. 5, as remarked by this distinguished authority, is a unique survival of triassic forms. It resembles the flat-sided whorls in Tirolites, and even certain earlier forms, like Popanoceras. It may be provisionally associated with this series until the sutures are known, since the shell is smooth, and similar to that of Psil. planorbe. This series should be carefully studied with ample materials. It may be that confusion exists between some forms now supposed to be true Psil. Hagenowi and some triassic forms still surviving in the Lias. Canavari, in his "Fauna del Lias Inferiore di Spezia," 1888, Plate VII., has figured a series of what appear to be true Tropites. These are very close congeneric forms of this triassic genus, and in our opinion should be referred to Tropites itself.<sup>3</sup> This gives greater force to the suggestion made above.

Canavari, in his "Fauna des unteren Lias von Spezia," gives some interesting forms of this genus. Psil. (Ægoc.), Plate XIX. Fig. 2, 4, 5, is a plicated form similar to pleuronotum. Psil. pleuronotum, Plate XIX. Fig. 3, may possibly be the same as Psil. calcimontanum, as stated by Wähner, but it is a dwarf, like most of the species from this locality. Psil. (Ægoc.) Portisi, Plate XIX. Fig. 6, appears to bear a similar relation to Psil. mesogenos. Wähner, however, considers it identical with the young of his Psil. Kammerkarense.

<sup>1</sup> Abhandl. geol. Reichsans. Wien, VII. pl. ii.

<sup>2</sup> Wähner's Psil. Struckmanni, Unt. Lias, Mojsis. et Neum., Beitr., IV. p. 196.

<sup>4</sup> Paleontogr., XXIX., and also Mem. del. Car. Geol. d' Italia, III., 1888.

<sup>&</sup>lt;sup>2</sup> The survival of characteristic triassic forms in the Jura shows that the connections between these two systems are closer than has been supposed, and gives support to opinions advocated in the chapter on Geological and Faunal Relations, and adds another group to the three already noted, Psiloceras, Lytoceras, and Phylloceras. These facts demonstrate that no insuperable barrier arrested the migration of forms and the continuity of the faunas in time. See remarks on Tropites in note to page 154.

#### TMÆGOCERAS.1

# Tmaegoceras latesulcatum, HYATT.

Amm. latesulcatus, HAUER, Ceph. d. Lias. d. Nordöstl. Alpen, pl. ix. fig. 1-3.

This extraordinary form, found in the red limestones of Adneth, has a combination of characteristics altogether distinct from that of any other species. The form of the whorl, its smooth shell, and the discoidal mode of growth, are purely psiloceran. The sutures are, however, arietian, and more like those of Caloceras than typical Psiloceras or those of any other genus. We are not aware of its having been found elsewhere than in the Mediterranean province. Hauer appears to think that its affinities may lie with the Arietidæ, and that is also our opinion, but until the young have been studied it cannot be classified.

# Tmaegoceras levis, HYATT.

Ariet. Levis, GEYER, Ceph. v. Hierlatz b. Hallstadt, pl. iii. fig. 10.

This is a smooth, keeled, and channelled discoidal form like the preceding, but dwarfish, like other species of this locality.

#### PLICATUS STOCK.

### SECOND, OR SCHLOTHEIMIAN BRANCH.

The living chamber is of uncertain length, though Quenstedt gives it in his "Ammoniten des Schwäbischen Jura" as possibly a volution in length in Schlotheimia. The shell is involute in some forms. The whorl is flattened laterally, and in old age became subacute. A smooth median zone or channel was formed on the abdomen by the suppression of the pilæ, which were continuous across the abdomen in the preceding nealogic or ephebolic stages. There are no geniculæ, though the pilæ are very completely developed. The forward bend is necessarily gradual, the whorl never having a sufficiently quadragonal form for the formation of abrupt bends or geniculæ on the edges of the abdomen. The sutures resemble those of Psiloceras and Caloceras.

#### WÆHNEROCERAS.2

The adult has a smooth median zone along the abdomen. The pilæ, so far as the young are known, cross the abdomen during the earlier nealogic stages, and this character is retained throughout the adult stages in some species. The smooth zone is really an incipient channel, formed subsequently by the resorption of the pilæ. This process may take place either in the later nealogic, ephebolic, or senile stage, according to the species. In old age the pilæ tend to degenerate into folds, and

<sup>&</sup>lt;sup>1</sup> Τμηγος, a furrow.

 $<sup>^2</sup>$  Dedicated to Dr. Frantz Wähner, as a token of respect for his remarkably accurate and instructive researches upon the Arietidæ.

become wider apart, the abdomen narrower, and the whorl consequently much compressed and subacute. No proper quadragonal whorl is formed during the growth, and therefore the senile outline of a section of the whorl is not trigonal, as in the senile stages of shells of other branches having a flattened abdomen and a keel in the ephebolic stages. All the species have true pilæ, though these are not prominent, and the earlier nealogic stages resemble adult specimens of the second subseries of Psiloceras, in which the folds are well developed and cross the abdomen. We cannot distinguish either this genus or Schlotheimia, or Caloceras, from Psiloceras by means of the sutures. Psil. sublaqueum, Wäh., and other species of Psiloceras having plications which cross the abdomen until a late stage of growth, are not distinguishable until they are nearly full grown from some discoidal forms of this series.

# Waehneroceras subangulare, HYATT.

Amm. subangulare, OPPEL, Paleontolog. Mittheill., p. 130.

We have referred the species to this genus entirely upon the information derived from notes made before Wæhneroceras was separated. It will be seen, however, that no species of Schlotheimia has young which remain similar to Psiloceras for such a prolonged stage as in Wæhneroceras.

One of the types of Amm. subangularis, Oppel, from Kalthenthal, in the collection at Munich, has a form similar to that of Psil. planorbe, and pilations which cross the abdomen. The young is also a pure planorbe until over 14 mm. in diameter. Another specimen from Filder, which we have referred also to this species, has curved and close-set pilæ, and the form and smooth abdomen of planorbe (not channelled at all) until over 26 mm. in diameter; then the pilæ begin to cross the abdomen. This last specimen was named Amm. planorbis by Oppel. There are also specimens from Hammerkhar, formerly referred by us to subangulare, which may be distinct. They certainly possess characters which were noted by us as intermediate between this form and true angulata, and one of them has a very peculiar old whorl, and may be a caloceran form.

# Waehneroceras tenerum, HYATT.

Ægoc. tenerum, Neum., Unterst. Lias, Abh. k. k. geol. Reichsans., VII. pl. iii. fig. 4, 5. Psil. tenerum, Wäh., Unt. Lias, Mojsis. et Neum., Beitr., IV. p. 198.

This form, described by Neumayr as occurring in the Northeastern Alps and also in Central Europe, at first seemed to us identical with *Wæh. subangulare*. Neumayr remarks that, though the young are so similar, the adults are separable, and we have upon his authority held it to be distinct. He also looks upon this species as very closely allied to *Psiloceras*, and to be a transition form from the latter to *Schlot. angulata*.

Species of this series have been figured by Wähner in Volume III. of his "Unteren Lias" as follows: Weeh. Paltar, Plate XXII., and Rahana, Plate XXIII.;

Proc. Bost. Soc. Nat. Hist., XVII., 1874, p. 18.

and in Volume II. he figures Weh. extracostatum, Plates XIV., XVI., and Panzneri, Plates XV., XXI. The figure of extracostatum shows an old whorl which is acute, but not involute. Among discoidal shells, Weh. circacostatum, Plates XV., XVI., curviornatum, Plate XVI., and haploptychum, Plate XVII., show that the whorls of their earlier nealogic and adult stages are without channels. Weh. anisophyllum, Plate XIX. Fig. 1 a, shows a very old stage with subacute trigonal whorl, and pilæ replaced by folds. Weh. megastoma, Plate XVIII. Fig. 2, 3, shows earlier nealogic stages with pilæ continuous across the abdomen in the adult and senile stages. Weh. euptychum, Plates XVIII., XX., stenoptychum, Plate XX., latimontamum, Plate XX., and diploptychum, Plate XXI., also belong to this genus. The last two are senile specimens, with subacute outer whorls, and all the above are discoidal shells exhibiting transitions from Psiloceras to Schlotheimia.

There are, however, involute forms in this series also figured by Wähner in the same work, but in Volume IV. These are Wæh. Guidoni, Plate XXVI. Fig. 3 a, b

(not Fig. 7), and Weh. Emmrichi, Plate XXVI. We doubt whether either of these involute forms can be regarded as transitional to Schlotheimia, as supposed by Wähner.

The results of our work upon the nealogic stages and their meaning in *Schlot. catenata*, and all other species, show that series arose only from discoidal shells, and probably never originated from the compressed and involute forms. These are themselves invariably discoidal and less compressed in their own young, showing them in every case to have been derived from shells having depress

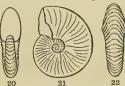


Fig. 20-22.— Views from in front, Emmirical and abdomen, of the young of Wath. Emmirichi, after Wähner, showing the involution of this species. The characteristic pile and channelless abdomen of this genus are also noticeable in these figures.<sup>2</sup>

to have been derived from shells having depressed abdomens and discoidal whorls.

Canavari, in his "Unteren Lias von Spezia," describes and figures dwarfs or the young of Weh. (Egoc.) Emmrichi under the name of Guidoni. Wähner thinks that Canavari's forms (Plate XVIII. Fig. 14, 15) are referable to his Guidoni, and Fig. 16 to be identical with his Emmrichi. The last is to us a very remarkable form, since it possesses continuous lateral and abdominal constrictions.

#### SCHLOTHEIMIA.

The form varies in this genus from discoidal to involute, but the umbilici are never entirely covered in. The whorls are usually flattened more or less on the sides, and the abdomen depressed. In the nealogic stages this form is common,

<sup>&</sup>lt;sup>1</sup> We have given outline figures of Wash. curviornatum, Summ. Pl. xi. fig. 7, haploptychum, fig. 8, toxophorum, fig. 9, and Emmrichi, fig. 10.

<sup>&</sup>lt;sup>2</sup> This figure, according to Wähner, is poorly drawn, the last volution too narrow, the umbilicus too open. It, however, exhibits the general aspect of involute forms in this series, and we have retained it with that purpose in view.

<sup>&</sup>lt;sup>3</sup> Paleontogr., XXIX., and Mem. del. Carta Geol. d' Italia, III., 1888

but in the adults of involute species the whorl is necessarily more compressed. The compressed stage occurs very early in the most involute species, the flattening of the sides and the depressed abdomen being omitted. A distinct median channel is formed on the abdomen in all species except some varieties of Schlot. catenata. The pilæ cross the abdomen in the earlier nealogic stages, but this peculiarity is rarely retained in adults except in catenata. The channel is formed by the suppression of the pilæ along the median zone of the abdomen, and is sometimes, especially in the young, supplemented by the bending inwards of the shell. This channel is converted into a smooth zone in old age by the degeneration and disappearance of the geniculæ, and the tendency of the abdomen to become narrower elevates this zone and makes the whorl subacute. Involution so far as known does not decrease in old age, and while it is easy to separate the senile stages of involute species from the senile stages of any species of Wæhneroceras, it is not practicable to distinguish those of the discoidal species until the ephebolic stages are studied. The specimens figured by Quenstedt 1 show that, in extremely aged specimens, the abdomen becomes in some cases rounded, and it is instructive to compare Fig. 10 m, Plate III., with the aged Psiloceras, Fig. 1 m, in order to see how complete the reversion occasioned by senility may sometimes become.

The sutures are not distinguishable from those of Wæhneroceras. They are perhaps less like those of Caloceras than those of that genus. The superior lateral lobes also are usually not so long and narrow, nor the superior lateral saddles so large and deep, nor the auxiliaries so much inclined posteriorly. The sutures are similar, both during the nealogic and senile stages, to those of Wæhneroceras, and the differences, if any can be detected, occur only in the adult stages.

Wähner's plates <sup>2</sup> are so complete, that one can study the history of the development of each form, and the relations of the species in their nealogic stages. The young of the more involute species, like Schlot. ventricosa and marmorea, are similar to the later nealogic stages of less modified and more discoidal forms, like Schlot. donar, and are also similar to the adult stages of still more modified species, like Schlot. angulata. These facts confirm the opinions we have advanced in the description above, and in other parts of this memoir.<sup>3</sup>

- <sup>1</sup> Amm. d. Schwab. Jura, pl. iii. and iv.
- Mojsis. et Neum., Beitr., IV., 1886.

<sup>&</sup>lt;sup>5</sup> We have several times referred in this memoir to extraordinary parallelisms. But we know of none more remarkable than those figured by Canavari in his "Fauna der Unteren Lias von Spezia." We refer to the genus *Ectocentriles* of Wähner, in which the young as described by Canavari are similar to Lytoceras, while the later nealogic and adult stages have the pilæ and abdominal channel of Schlotheimia.

### FIRST SUBSERIES.

### Schlotheimia catenata, Wähner.

Summ. Pl. XI. Fig. 3.

Amm. catenatus, Sow., De la Beche, Traité de Géol., p. 407, fig. 67.

Amm. catenatus, D'Orb., Terr. Jurass. Ceph., p. 301, pl. xciv.

Ægoc. catenatus, Wright, Lias Amm., p. 320, pl. xix. fig. 5–7; pl. xvii. fig. 3–6.

Schlot. catenata, Wäh., Unt. Lias, Mojsis. et Neum., Beitr., IV., 1886, p. 196.

Ægoc. subangulare, Wäh., Unt. Lias, Mojsis. et Neum., Beitr., IV., 1886, p. 162.

Amm. angulatus thalassicus, Quenst., Amm. Schwab. Jura, pl. ii. fig. 9 (not fig. 4, 5).

Amm. angulatus psilonotus, Quenst., Ibid., pl. ii. fig. 10, 11.

Amm. angulatus hircinus, Quenst., Ibid., pl. ii. fig. 12.

Amm. angulatus oblongus, Quenst., Ibid., pl. ii. fig. 6.

Ægoc. angulatus, Neum., Unterst. Lias, Abhandl. geol. Reichsans., VII. p. 33, pl. ii. fig. 5.

Ægoc. subangulare, Neum., Ibid., p. 33.

Localities. — Chevigny near Semur, Balingen, Diebrook near Ravensburg, Mühlhausen, Coppenbrügge in Westphalia, Hildesheim, Markoldendorf.

In the collection of the Museum of Stuttgardt from the Planorbis bed there is a specimen of this species, which is more discoidal than Schlot. angulata, and more like Wæhneroceras in its aspect than any other members of this series, and the same facts are observable in Quenstedt's collection. In the collection at Semur there are three specimens from the Planorbis bed correctly named catenatus. They are not large, and one specimen at the diameter of 52 mm, shows signs of old age in its obsolescing pile and smooth abdomen. We have also examined D'Orbieny's types and confirmed these comparisons. Neumayr compares his specimen from the Planorbis bed of Pfonsjoch with the North German species of angulatus, which is a true catenatus, and in Professor Emerson's collection from Markoldendorf, now at Amherst, Mass., all specimens of this species agree very closely with catenatus as figured by Quenstedt. The pilæ cross the abdomen with a forward bend, but in one precisely the peculiarities of Quenstedt's Fig. 12 are exhibited, the pilæ being straight as they cross the abdomen. Amm. ang. oblongus, Quenst., may be a large variety; the whorl as figured resembles that of catenata.

# Schlotheimia striatissima, HYATT.

Amm. angulatus striatissimus, QUENST., Amm. Schwab. Jura, pl. iii. fig. 2.

Amm. angulatus striatus, QUENST., Ibid., pl. iii. fig. 3-5.

Locality.— Semur.

Two specimens of this species in the Museum of Comparative Zoölogy and Quenstedt's descriptions and figures show that it is a discoidal shell like catenata, but the abdomen is narrower, the whorl more compressed, and the pilæ more numerous and finer than in that species. They remind one in this respect of the second subseries, but unfortunately there are no transitional modifications by which to follow out the connection, if it existed, with these dwarfed forms of the Oxynotus bed. The mould of the young specimen supposed by Quenstedt to

have probably come from the "gelbesandstein" of the Trias, near Tübingen, belongs to this species, and it contains also other discoidal varieties, as well as the extraordinary compressed but still discoidal form of *striatissimus*, Quenst.

# Schlotheimia colubrata, HYATT.

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Amm. colubratus, Ziet., Verst. Würt., pl. iii. fig. 1.
Amm. Moreanus, D'Orb., Terr. Jurass. Ceph., pl. xciii.
Amm. Moreanus, HAUER, Ceph. Nordöstl. Alpen, pl. xv. fig. 1, 2 (not fig. 3, 4).
Ægoc. Moreanus, Wright, Lias Amm., p. 322, pl. xvii. fig. 1, 2.
Amm. angulatus Thalassicus, Quenst., Amm. Schwab. Jura, pl. ii. fig. 4, 5 (not fig. 9).
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Localities. - Deyrolay, Hanover.

In the Semur collection there is a specimen named *Moreanus* from the lower part of the same zone with *Liasicus*, and it may be said to agree with D'Orbigny's figure.<sup>1</sup> This is a variety identical with *colubratus*, Ziet., growing to a larger size than *catenatu*. At the diameter of 168 mm. in this specimen, the pilæ crossed the abdomen, showing that old age had set in. That this is sometimes a nealogic feature retained throughout life is shown by another specimen, which at the diameter of 21 mm. has the pilæ continued across the abdomen.

### Schlotheimia angulata, ZITTEL.

Summ. Pl. XI. Fig. 4.

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Amm. angulatus, Schlot., Die Petrefactenkunde, p. 70.

Amm. angulatus depressus, Quenst., Amm. Schwab. Jura, pl. ii. fig. 1, pl. iii. fig. 9.

Amm. angulatus costatus, Quenst., Ibid., pl. ii. fig. 8.

Ægoc. angulatus, Wricht, Lias Amm., pl. xiv. fig. 5, 6.

Schlot. angulata, Zittel, Handb d. Paleont., I. p. 456, fig. 637.

Schlot. angulata, Wähner, Unter. Lias, Mojsis. et Neum., Beitr., IV., 1886, p. 163, pl. xix. fig. 1-3, pl. xx. fig. 1-6.

Localities. — Muhlhausen, Hildesheim, Lyme Regis.
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The young appear to be smooth for about one and a half whorls, then lateral tubercles appear. These spread upon the sides into folds, which on the early part of the fourth or last of the third whorl rapidly become true depressed pilæ, and then begin to be continued across the abdomen with a very decided forward bend at the geniculæ, and form an acute angle on the abdomen. The depression which obliterates the angle of intersection of the pilæ on the abdomen and forms the smooth zone begins on the last half of the fourth whorl.

On the early part of the fourth whorl the abdominal lobe is somewhat deeper than the superior laterals, and these again very much deeper than the inferior laterals. The saddles are broad and shallow, the superior laterals being a trifle shallower than the inferior laterals. On the first quarter of the fifth volution the bases of the superior and inferior lateral saddles and the tops of the superior lateral lobes have become trifid, or unequally divided, whilst those of the inferior lateral lobes and auxiliary saddles are equally divided. The abdominal lobes are shorter than the superior laterals, though the saddles maintain

 $<sup>^1</sup>$  The original at the Jardin des Plantes is a fragment, and D'Orbigny's figure is in large part  $\pi$  restoration, especially with regard to the internal whorls.

their old proportions. In the full adult condition the characteristics of the sutures differ considerably from those of the typical Arietidæ, and approximate to those of Psiloceras.

The seventh whorl increases in size with great rapidity, the abdomen becoming narrower, the channel shallower, the pilæ more depressed, losing their prominent somewhat abrupt genicular bend, and on the abdomen becoming depressed to a level with the siphonal line. The involution of this whorl is about two fifths, and that of the ninth a trifle over one half. The peculiar flattening of the sides and form of the adult whorl, and the amount of involution, are close approximations to the adult characteristics of Amm. Charmassei, but the septa are different and the young more robust; the pilæ are developed earlier and more rapidly, and the abdominal channel also. In some specimens, however, these last are not noticeable until quite a late period, the pilæ being continuous across the abdomen, as in Der. planicostum, even on the sixth volution.

In the collections at the Stuttgardt Museum are several very fine specimens of the old age of this species, and it is easy to distinguish it from *Charmassei* by the narrowness of the whorls and its more open umbilicus and discoidal aspect. One of the largest of these measures 495 mm., the last whorl 17 mm.; another measures 515 mm., and the last whorl 18.5 mm.

In the Museum at Stuttgardt, in the centre of a crushed specimen of the true angulata from Kirchheim, the young was very clearly exposed. This had very smooth and round, though rather stout whorls. The pilæ appeared on the sides as faint folds, which are straight at first, then curve, reach the abdomen, and finally cross it with a forward inflection. These become very prominent and decided before the channel is formed, which finally cuts through the pilæ. This variation, however, is considerable, since in the adult of this specimen the channel is only partially developed, the pilæ being only about half cut through, though the specimen is about two and one fourth inches in diameter. There is here a close likeness to some of the trias forms, but not to the true planorbe, which the young does not resemble closely. They resemble Wæhneroceras very closely. The same relations were observed in young specimens in Professor Quenstedt's collection, and in the Museum of Comparative Zoölogy.

It often occurs, also, that after the channel is developed, and the shell is quite large, the pile again cross the abdomen, but this is not so frequent as has been supposed. They oftener remain separate until old age.

The original of *Amm. angulatus*, Sow., which we saw in the British Museum, is only a malformed *communis*.<sup>1</sup>

<sup>&</sup>lt;sup>1</sup> See also Wright, Lias Amm, p. 473.

### Schlotheimia Charmassei, Wähner.

Summ. Pl. XI. Fig. 5.

Amm. Charmassei, D'Orb., Terr. Jurass. Ceph., p. 296, pl. xci. (not pl. xcii.).
Amm. angulatus compressus, QUENST., Amm. Schwab. Jura, pl. ii. fig. 2.
Amm. angulatus compressus gigas, QUENST., Ibid., pl. iv. fig. 2.
Schlot. Charmassei, Wäh., Unt. Lias, Mojsis. et Neum., Beitr., IV. p. 196.
Ægoc. Charmassei, Wright, Lias Amm., p. 323, pl. xx. fig. 1-3.

Localities. - Semur, Lyme Regis, Tübingen.

Besides the characteristics mentioned in the description of angulata the following may be added. On the sixth volution, the extremely gibbous form of the young begins to change. The whorl increases more rapidly, the abdomen is narrower, and the pile as in preceding species, with this exception. On this volution, or perhaps on the fifth, they become bifurcated, or else have intermediate short pile interspersed between the longer ones. The sutures have remarkably large abdominal lobes, shallower than the superior laterals, but with much more ragged outlines. The siphonal saddle is extraordinary in this respect. It is very large, and marked with several lateral minor lobes and saddles. The remaining lobes and saddles are more complicated than in angulata.

On the sixth volution, the form of the whorl changes more than in angulata. The involution of this whorl equals one half of the side of the sixth, whereas in angulata the envelopment does not equal this until it reaches the ninth volution. The involution at the same age in this species, i. e. on the ninth whorl, covers full two thirds of the side of the eighth whorl. There is a form in Professor Fraas's collection from Möhringen answering to the young of Charmassei, as figured by D'Orbigny, Plate XCI., and another from Filder, which is precisely intermediate in its characteristics between this and the smoother, flatter variety figured on Plate XCII. The oldest specimens in the possession of the Museum of Stuttgardt measured 53 mm., and the last whorl 23 mm. Schlot. angulata parts with its pile and grows smooth much earlier apparently than Charmassei. Possibly this occurs at about the same age, but the superior size of Charmassei makes it seem older when the senile characteristics begin to appear.

#### Schlotheimia Leigneletii, Wähner.

Amm. Leigneletii, D'Orb., Terr. Jurass. Ceph., p. 298, pl. xoii. Schlot. Leigneletii, Wäh., Unt. Lias, Mojsis. et Neum., Beitr., IV. p. 197. Amm. compressus (pars), QUENST.

Localities. - St. Thibault, Semur, Vaihingen, Stuttgardt, Behla.

The same class of facts divides this species from *Charmassei* that we used above to show the differences between the latter and *angulata*; namely, that the young differ as well as the old in some specimens.

The differences are very great between the fifth whorl of *Leigneletii*, and the same age in *Charmassei*. The tubercles are more prominent on the edge of the abdomen, the pilæ more depressed on the sides, and their terminations tubercular on the edge of the abdomen, which, instead of being a broad, rounded space, is a

flattened zone. The reduction of the abdomen of course occurs in all species of this group, but in other species, except *Boucaultiana*, it is found only during the senile stage.

Amm. angulatus compressus of Quenstedt may also in part belong to Charmassei, since two specimens from the Stuttgardt Museum of this name apparently belong to this species only. The envelopment in one of these specimens covers about two thirds of the sides of the eighth whorl, and about the same age the pilæ again cross the narrow abdomen, obliterating the median depression or smooth zone, and introducing a series of crenulations instead. This is a return to the young condition, and indicates the first degradational or clinologic stage. It is not intended by this to deny that there are no young which closely approximate to the young of Charmassei. On the contrary, some specimens are apparently identical in all respects, except the greater flatness of the whorls and the earlier period at which involution appears, and the two species are connected by numerous transitional forms.

### Schlotheimia Boucaultiana, Wähner.

Summ. Pl. XI. Fig. 6.

Amm. Boucaultianus, D'Orb., Terr. Jurass. Ceph., p. 294, pl. xc. Schlot. Boucaultiana, Wäh., Unt. Lias, Mojsis. et Neum., Beitr., IV. p. 196. Ægoc. Boucaultiana, Wright, Lias Amm., p. 327, pl. xviii. fig. 1-4.

Locality. - Semur.

This remarkable species differs from Leigneletii in about the same manner that the latter differs from Charmassei, in other words, it is more involute than Leigneletii at the same age; i. e. on about the seventh or eighth whorl at least three fourths of the sides are hidden. The pilæ are not so coarse as in that species, and the abdominal channel is obliterated at an earlier age and is succeeded by crenulations caused by the pilæ. The sutures differ considerably. The specimen examined was one of D'Orbigny's types. The same transitional forms which lead into Leigneletii also lead into other more compressed and more involute forms which are transitional to the true Boucaultiana. They differ from Leigneletii only in the suppression of the tuberculated pilæ, and a general tendency toward obsolescence of the pilæ on the sides.

### Schlotheimia D'Orbignyana, HYATT.

Amm. Charmassei (pars), D'Orb., Terr. Jurass. Ceph., pl. xcii. (not pl. xci.)

Locality. — Semur.

This species has depressed pilæ and resembles closely *Boucaultiana*, but is not so involute. It is in fact, as described by D'Orbigny, an extreme modification of *Charmassei*, with excessively compressed whorls, and acquiring in the clinologic stage a subacute abdomen. It resembles more closely *Schlot. ventricosa* of Wähner than it does any other species, but it is even more compressed and more like *Charmassei* in the adult stage than that species. D'Orbigny's figure is that of an old shell; the adults are less acute and more like *Charmassei* or *Leigneletii*.

The forms figured by Wähner in his "Unteren Lias" may be divided into three subseries. It was not practicable to determine whether these series were artificial or natural, though many figures of the young were given by Wähner.

The first series can be distinguished by the finer pilæ and somewhat compressed whorls. They are as follows. Schlot. catenata, Wäh., and angulata, in the Planorbis bed. The following, though still discoidal, are slightly more involute forms, if one can say this after comparison with Neumayr's figure of angulatum from Pfonsjoch.<sup>2</sup> They are Schlot. montana, Wäh., Plates XIX., XX., Donar, Plates XIX., XXI., extranodosa, Plate XX., pachygaster, Plate XXI., and marmorea, Plate XXII., and all occur in the Megastoma and Marmorea beds.

The second or coarsely pilated series have more gibbous forms in the young and much deeper channels, or, in other words, the pilæ have more prominent terminations on the abdomen. The discoidal forms are as follows. Schlot. ind., Plate XVIII. Fig. 4, which has in an exaggerated condition the characteristics of the subseries, and may be a pathological specimen, taurina, Plate XIX. Fig. 5, angulata, var. ind., Plate XX. Fig. 5. All three of these were found in the Megastoma and Marmorea beds, but were followed by two young forms occurring, according to Wähner, in the Rotiformis beds. These are Schlot. scolioplycha and posttaurina, Plate XXIII., and appear to have been the young of species, which may have been more involute in the adults.

The third subseries has young with even stouter whorls than in the second subseries, though not otherwise separable. *Schlot. trapezoidale*, the first species, occurred, according to Wähner, in the Marmorea bed, and was succeeded by *ventricosa*, Plate XXIII., and an undetermined form, Plate XXIII. Fig. 12, both in the Rotiformis bed.

Canavari in "Unteren Lias von Spezia" describes dwarfs or young of Schlot. (Ægoc.) trapezoidale, Plate XVIII. Fig. 8, 9, and ventricosum, Plate XVIII. Fig. 10, which seem to be identical with forms described by Wähner; also Schlot. (Ægoc.) catenalum, Fig. 1, comptum, Fig. 3–5, Collegnoi, Fig. 6, all of which are very closely allied, and may be either young or dwarfs of Schlot. Charmassei, or the more involute varieties of Schlot. angulata.

#### SECOND SUBSERIES.

The abdominal channel is narrower and deeper proportionally than in the first subseries, and is a true furrow, in place of being a smooth zone or mere depression formed between the interrupted pilæ, as in Wæhneroceras and in the first subseries of Schlotheimia. The shells known are finely pilated, and the furrow is similar to what it is in the young of some species of the first subseries. The species have been found only above the Bucklandi zone, and are all, so far as known, dwarfs.

Mojsis. et Neum., Beitr., IV., 1886.
 Abh. k. k. geol. Reichsans., VII., pl. ii. fig. 5.
 See Schlot. trapezoidale, Wäh., Mojsis. et Neum., Beitr., IV. pl. xxiii. fig. 2 c, and others on the same plate.

# Schlotheimia rotunda, HYATT.

Amm. lacunatus rotundus, QUENST., Amm. Schwab. Jura, p. 167, pl. xxii. fig. 5, 6.

This shell is more discoidal than any others described below. The whorls are also stouter as a rule. The pilæ on the umbilical shoulders are coarser and are tuberculated according to Quenstedt's figures and descriptions. *Amm. lacunoides*, Quenst., may be the young of this or an allied species. It occurs so far as now known only in South Germany.

### Schlotheimia lacunata, HYATT.

Amm. lacunatus, Buckman, Murch. Geol. Cheltenh., 2d ed., p. 105, pl. ii. fig. 4, 5.

Amm. lacunatus, Quenst., Amm. Schwab. Jura, p. 167, pl. xxii. fig. 1-4.

Amm. lacunatus, Duм, Étud. Pal. d. Bas. d. Rhone, p. 120, pl. xxi. fig. 18-20.

Атт. lacunatus, Wright, Lias Amm., p. 330, pl. lvi. fig. 16-18.

Amm. deletum, Canavari, Lias v. Spezia, Paleontogr., XXIX. pl. xviii. fig. 13.

Amm. sp. ind. cfr. lacunata, CANAVARI, Fauna del Lias, Mem. del. Carta Geol. d' Italia, III., 1888.

Localities. - St. Thibault, Semur.

The pilæ are not coarse or tuberculated at the umbilical shoulders. The whorl is also more compressed and the involution greater than in Schlot. rotunda, covering about two thirds of the side. The young according to the figures given are also not smooth to so late a stage as in that species. The description of the originals in the Geology of Cheltenham in a measure makes up for the figures. The latter belong to a discoidal species, the former gives the usual combination of an involute shell, narrow abdomen, flattened sides, and half-concealed whorls. An important statement is also added, that the "ribs" cross the abdomen in the young. The latter indicates the possibility of a direct derivation of the second subseries from Schlot. catenata, and also serves to confirm the identification of Wright's species with this, since Wright mentions the same characteristics.

# Schlotheimia Geyeri, HYATT.

Schlot. lacunatus, Geyer, Liasis. Cephal. v. Hierlatz b. Hallstadt, p. 259, pl. iii. fig. 22, 23.

This species has fine but sparsely distributed pilæ at the umbilical shoulders which speedily divide into two or more finer pilæ. The abruptness of the division gives the umbilical pilæ a resemblance to those of *Schlot. Quenstedti* in Geyer's figures, but there are no tubercles, and the involution covers about four fifths of the side, and the whorls are considerably compressed.

### Schlotheimia angustisulcata, GEYER.

Schlot. angustisulcata, GEYER, Liasis. Ceph. Hierlatz b. Hallstadt, p. 256, pl. iii. fig. 24, 25.

The pilæ are finer, the whorls more compressed, the involution quite as extensive as in the preceding. The sutures which are figured in this species, if they can be correctly given in so small a figure, are quite distinct from those of the similar involute forms of Schlotheimia.

<sup>1</sup> Amm. Schwab., p. 162, pl. xxi. fig. 24, 25.

# Schlotheimia Speziana, Canavari.

Ægoc. Spezianum, Canav., Unt. Lias'v. Spezia, p. 166, pl. xviii. fig. 12. Schlot. Spezianum, Canav., Fauna del Lias, Mem. del. Carta Geol. d'Italia, III., 1888.

This form is more compressed, has different pilations, and a remarkably narrow channel. It is also as involute as any other species of this subseries, and appears in the drawing to exceed all other forms in this respect.

### THIRD, OR VERMICERAN BRANCH.

The living chamber is in most species attenuated, cylindrical, at least a volution in length, and sometimes over one and a half volutions. The shell in the majority of forms is discoidal, and the area of envelopment almost invariably limited to the abdomen. During the senile stages, the whorl tends to acquire smooth, rounded, and convergent sides, and frequently loses the keel and channels, thus completely reverting to the smooth cylindrical form of the young. The sutures in each separate series tend to increase in the depth and breadth of the second lateral saddles in the higher species, and there is a backward trend of the auxiliary lobes and saddles which is strongly marked in some forms. In Vermiceras the sutures become more decidedly arietian, the abdominal lobe is deeper and narrower, the lateral lobes are broader and less dendritic, and the auxiliary lobes and saddles are not as a rule inclined posteriorly.

### CALOCERAS.

The shells are extremely discoidal, with numerous almost cylindrical whorls which often retain the nealogic form throughout life. The pilæ are curved, and they usually have an immature fold-like character, in keeping with the arrested development of the form in the adult whorls. They also do not have well defined geniculæ, and in some species they may be straight, and even tuberculated. The sutures usually have longer and narrower lobes, deeper saddles, and more complicated margins than in Psiloceras. They are, however, hardly distinguishable generically from those of some species of that genus, which occur in the Northeastern Alps, and in some species also they approximate to those of Vermiceras. The range of form and characteristics is very great, as might be imagined, in a group which is transitional from Psiloceras to the true Arietidæ.

#### First Subseries.

The whorls are rounded and gibbous, the keel when present not prominent; the channels absent or appearing merely as smooth, inflected zones; the pilæ fold-like, and without geniculæ or tubercules. The sutures are very variable, some having more complicated margins, as in the Psiloceratites of the Northeastern Alps, and others approximating more nearly to the simplicity of *Psil. planorbe* of Central Europe. The abdominal lobe, however, as in Psiloceras, is not usually deeper than the superior laterals.

### Caloceras Johnstoni, HYATT.

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Amm. Johnstoni, Sow., Min. Conch., p. 464, pl. cccexlix.
Amm. torus, D'Orb., Pal. Française Ceph., p. 212, pl. liii.
Amm. psilonotus plicatus, Quenst., Amm. Schwab. Jura, pl. i. fig. 12, 13.
Amm. Johnstoni, Quenst., Ibid., pl. i. fig. 20.
Ægoc. Johnstoni, Wright, Lias Amm., pl. xix. fig. 3, 4.
Ægoc. Belcheri, Wright, Ibid., pl. xix. fig. 1, 2 (not pl. xv. fig. 7-9).
Ægoc. Johnstoni, Neum., Unterst. Lias, Abhandl. geol. Reichsans. Wien, VII. pl. iii. fig. 2.
Ægoc. Johnstoni, Wäh., Unt. Lias, Mojsis. et Neum., Beitr., IV. pl. xvi. fig. 6-9.
Localities. — Wiesloch near Heidelberg, Bristol, Cheltenham.
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This form differs from *plunorbe* in the outline of the whorl, which is much narrower, more rotund and gibbous laterally, and in the greater prominence of the pilæ.

A specimen in the Museum of Stuttgardt measuring 120 mm., labelled tortilis, Nürtingen, has a living chamber still incomplete, though nearly one volution in length. Abdomen is slightly more elevated than in typical adult torus and the sides more inclined, as is usual in old age of this species. Otherwise the form and pilæ, especially in the umbilicus, are the same.

Sutures of adult are similar, as far as seen, to those of Psiloceras, and in old age the lobes and saddles decrease in size, becoming simpler in outline. Quenstedt's specimen, figured in "Ammoniten des Schwäbischen Jura," Plate I. Fig. 20, is 110 mm. in diameter and shows the effects of senility in the compressed whorl. His Figure 13 shows the living chamber to have been at least one volution in length. The typical forms of this series are found in the Northeastern Alps, but the distribution is general, as has been already noted by Neumayr.

In the collection of the Sorbonne at Paris there is one specimen from Beaure-gard precisely similar to that figured by D'Orbigny, except that the whorls are much larger and stouter. In the collection at Munich there are specimens from Pfonsjoch, Kander in Bresgau, and Lyme Regis, exhibiting the typical form of Johnstoni until they reach the diameter of 145 mm.

### VAR. Beauregardiense.

Amm. Beauregardiensis, Collenot.

This form from Beauregard in the collection at Semur is 185 mm. in diameter, and has whorls increasing more rapidly in size than in the typical *Johnstoni*, but otherwise does not differ from that species.

## Caloceras tortile, HYATT.

Plate I. Fig. 12-14. Summ. Pl. XI. Fig. 14.

This species is very generally misinterpreted by German and English paleontologists. The young have exactly the same broad, gibbous whorl as the young of the keelless Johnstoni, but gradually become elevated a little on the abdomen, and at the same time acquire a faint keel. Subsequently the abdomen becomes more elevated, and slight channel-like inflections appear on either side. At the diameter of 98 mm. this occurred in one specimen from Beauregard in the collection at Semur. At the diameter of 195 mm. in other specimens from Beauregard, the faint channels had disappeared, the pilæ were nearly obsolete, and the keel not so distinct. The marginal digitations of the lobes and saddles were also deeper and much changed. At the diameter of 270 mm. senile changes were far advanced in the only specimen of this size yet studied. The abdomen had become rounded and keelless, and the pilæ so nearly obsolescent as to be barely distinguishable.

A specimen from Beauregard in the collection of the Sorbonne, under the name of *Anm. laqueolus*, Schlönbach, must have been when complete about 200 mm. in diameter. The outer whorl of this shell resembles a typical *tortile*, with depressed abdomen and keel. The abdomen at earlier stages in the same specimen is rounded. *Laqueolus*, Schlönbach, is not of this species, but belongs to *Cul. Liasicum*.

In some specimens the abdomen changes from rounded and rather flattened in the young to a more angular outline in older stages, but does not acquire a keel. This occurs in D'Orbigny's original at the École des Mines, and in specimens labelled *tortilis* from Chalandry, in the collection of the Sorbonne, at sizes varying from 22 to 55 mm. It is probable that a well defined keel never made its appearance even in the adults in some of these specimens.

#### VAR. raricostatoides.

There are two specimens in Quenstedt's collection from Quedlinburg, three in the Museum of Comparative Zoölogy, and others at Semur, all found in association with *Planorbis*. These seem to be identical with the forms described by Dunker in the "Paleontographica" as *Amm. raricostatus*.

A part of the specimens identified by Oppel as Johnstoni in the Munich collection appear to belong to Cal. tortile. One specimen especially is a rather compressed form, from Waldenburg, with a slight keel developed at a late stage of growth, and at the same time there is a change of form in the whorl, which approximates to the parallel-sided, flattened-abdomened, carusense-like varieties of Cal. Nodotianum; the pilæ also begin to wear a more advanced aspect.

The torus-like variety is finely represented in the Bristol Museum by specimens from Cotham, and a form which appeared to be the same was reported as coming from the Bucklandi bed at Ashley Down. This has somewhat stouter whorls than the earlier forms at the same age, and shows the same tendency to become stouter and larger manifested in the later occurring species of other progressive series. The young have the usual development of tortile, in some instances producing a decided keel, and in others merely a slightly more compressed form in the adult or old, the abdomen remaining keelless. They have straight pilæ, and look remotely like raricostatus in form, but the young have

the usual stout smooth whorl of the young of Johnstoni. Quenstedt places them with laqueus, but this, we think, is a mistake, arising from not giving proper weight to the characteristics of the nealogic stages.

The presence of this form in the North German basin is worthy of remark, since it is a degraded variety. The transitional keelless varieties uniting this species and Johnstoni would have been considered distinct under the name tortile, while the keeled forms would have been separated and designated as a distinct species, but for the fact that similar variations are also represented within two other species, Cal. Liasicum and Nodotianum. It is evident from this, that the keel in Caloceras has not become an hereditary character, but is a morphological equivalent in varieties of different species.

#### Caloceras Liasicum.

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Amm. Liasicus, D'Orb., Pal. Fran. Ceph., I. pl. xlviii.
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Amm. Liasicus, Hauer, Ceph. Lias Nordöstl. Alpen, pl. iii. fig. 1-3.

Amm. sironotus, Quenst., Handb. Pet., p. 432, pl. xxxvii. fig. 1; and Die Amm. Schwab. Jura, p. 23, pl. i. fig. 21.

Amm. laqueolus, Schlön., Paleontogr., XIII. pl. xxvi. fig. 1.

Ægoc. laqueolus, Wright, Lias Amm., p. 315.

Ægoc. Liasicum, Wright, Ibid., pl. xv. fig. 1, 2; pl. xvi. fig. 1, 2.

Ægoc. tortile, Wright, Ibid., pl. xv. fig. 10, 12.

Ariet. Liasicus, Wäh., Unt. Lias, Mojsis. et Neum., Beitr., VI., 1887, pl. xx. fig. 1-5.

Localities. - Semur, Bristol.

A large specimen in the Tübingen collection, about 100 mm. in diameter, shows by comparison with D'Orbigny's figure that sironotus, Quenst., is probably identical. One specimen at Semur retained very gibbous sides and broad abdomen to a diameter of 175 mm., and then formed an elevated abdomen without acquiring a true keel as figured by D'Orbigny. Another shell had reached the diameter of 260 mm., but no true keel was formed, though old age began to show its approach in the obsolescence of the pile. In D'Orbigny's collection these very broad forms stand side by side with the narrow one figured by him, which is identical with *sironotus*, Quenst. D'Orbigny's original has the keel as well developed at a diameter of 100 mm. as the broad variety at a diameter of 250 mm. A comparison of the young with the young of tortile showed that they are closely allied by their development. No constant distinction exists, except that Liasicum is usually a stouter shell, and has about the same relation to tortile that the stouter forms of carusense in the Upper Bucklandi bed have to those of the same name in lower beds. Wähner's work upon this species gives figures of the young, and exhibits a close alliance with Cal. Johnstoni. The keel appears in his Figure 3 b, in a small but probably full-grown specimen, but no channels are noted in his figures or description.

The extraordinary series of forms discovered by Neumayr and Wähner in the Northeastern Alps enable us to give the following list of species, arranged in subseries.

Cal. (Ægoc.) Johnstoni, as figured by Wähner, Mojsis. et Neum., Beitr., IV., Plate XVI. Fig. 6-9, and Neumayr, Unterster Lias, Plate III., show that the typical coarsely pilated form of the Central European province exists also in the Northeastern Alps, but has probably a more limited number of descendants in that fauna. A not infrequent but very interesting variation in this species is the torus variety, also present in the Northeastern Alps, Neum., Ibid., Plate III., and Wähner, op. cit., Plate XVI. Fig. 6. It is distinguished by a marked tendency to sudden increase in the size of the whorl by growth at a late nealogic stage. The next gradation in the subseries, as exhibited in the Northeastern Alps, is a species having a still quicker increase in bulk, as described by Wähner, Cal. (Ægoc.) hadroptychum, Ibid., Plate XVIII. Fig. 1-3. The increase in the whorl takes place quite early, and the coarse fold-like pilæ and rather broad whorls indicate the next step in gradation to be, as pointed out by Wähner, the unnamed form figured on his Plate XVII., which leads, as also pointed out by the keen eyes of this author, into the remarkable Cul. (Ægoc.) nigromontanum given on Plate XXIV. The affinity is better shown by the young figured on Plate XXV. Fig. 2, which is very similar to the adult of the preceding species. This species has a distinct but broad keel in the adult, and slightly compressed whorls similar to those of Cal. proaries, and is a good example of morphological equivalence. Cal. Liasicum, as described and figured by Wähner, evidently has compressed whorls, and is more closely allied to Cal. Johnstoni in all varieties than the same species in Central Europe.

Cul. (Ariet.) Loki<sup>2</sup> has close relations to Liusicus of the Northeastern Alps, as pointed out by Wähner, and Cal. (Ariet.) Seebachi<sup>3</sup> is also an allied species.

#### SECOND SUBSERIES.

The whorl is subquadragonal in the adult. An obtuse keel is always present. Very shallow channels are developed, and the pilæ are prominent, straight, and in some species have slight geniculæ like those of Vermiceras.

The sutures, with the exception of *Cal. laqueum*,<sup>4</sup> have an abdominal lobe deeper than the superior laterals, but the superior and inferior lateral lobes are of nearly equal size and length, the superior lateral saddles broader, but of about the same depth as the inferior laterals, and the marginal lobes and saddles similar to those of *Psil. planorbe*.

The young are similar to *Cal. Johnstoni*. The clinologic period has a subacute abdomen, but this becomes rounded in the last part of the senile stage. The lobes in this stage return to their younger or psiloceran proportions, the abdominal lobe becoming shallower and broader, the lateral lobes narrower and shorter, and the lateral saddles broader and shallower in proportion.

<sup>&</sup>lt;sup>1</sup> Mojsis, et Neum., Beitr., VI. pl. xx. 

<sup>8</sup> Ibid., V. pl. xxi. 

<sup>8</sup> Ibid., V. pl. xx.

<sup>&</sup>lt;sup>4</sup> Cal. laqueum seems to have an abdominal lobe shorter than the inferior lateral lobes, and in some specimens the sutures are similar to those of the first subseries. In other specimens they resemble more closely those of Psil. planorbe, and in still others they become similar to the sutures of Vermiceras.

# Caloceras laqueum, HYATT.

Summ. Pl. XI. Fig. 22.

Amm. Iaqueus, Quenst., Amm. Schwab. Jura, pl. xviii. fig. 4; pl. i. fig. 14 (not fig. 15, 16). Amm. intermedium, Portl., Geol. Londonderry, p. 136, fig. 17.

Ægoceras intermedium, Wright, Lias Amm., p. 314, pl. xv. fig. 3, 4 (not fig. 5, 6).

Ægoceras Belcheri, Wright, Ibid., p. 313, pl. xv. fig. 7-9 (not pl. xix. fig. 1, 2).

Ariet. Scylla, Wäh, Unt. Lias, Mojsis. et Neum., Beitr., VI. 1887, pl. xxv. fig. 7, 8.

Amm. Scylla (pars), Reynés, plates.

The youngest specimen I have yet seen of this species was 26 mm. in diameter. The abdomen, however, was smooth, with no indications of the immature keel of the adult, the sides exceedingly gibbous. The pilæ evidently began early, and were closely crowded and slightly curved forwards.

In one specimen the pilæ were very slightly developed in the adult; in another, at a corresponding size, they were already disappearing, and upon the next or senile whorl they were almost obsolete. The keel probably becomes very slight at this time, and the likeness to its own young must then have been remarkably close.¹ This specimen was 53 mm. in diameter.

The similarity of the adult of this species to the young of Ver. spiratissimum is unmistakable. A specimen from Bebenhausen, in Quenstedt's collection, shows that the sutures are intermediate between those of Cal. Johnstoni and those of Ver. spiratissimum. The young of a specimen from Oestringen in Fraas's collection, Stuttgardt Museum, when about 26 mm. in diameter, has the exact form and characters of Quenstedt's figure, but no signs of a keel, though this appears soon afterwards. A fine series in the Semur Museum shows that the keel may not yet have arisen in a specimen at the diameter of 45 mm. The whorl also at the time of the appearance of the keel may have either a broad, depressed abdomen, as in the varieties which approximate to the young of Ver. spiratissimum and carusense, or this part may be elevated, as in Cal. tortile.

The young, however, are like the young of Cal. Johnstoni. The sutures also vary in the same way, some specimens having sutures like those of Johnstoni, and others approximate to those of carusense and spiratissimum. Old age in all these was marked by narrowing of the abdomen, loss of the keel, etc., which probably precedes a rounding off of the same region, though this extreme effect of senility was not observed. The pilæ often cross the abdomen in the young, but not in the adult. In one specimen, however, which had the senile angularity of the abdomen well marked at the diameter of 73 mm., the pilæ again crossed the abdomen, and then faded out almost entirely. Another specimen, even at the extreme diameter of 105 mm., retained a keel, as in the adult.

Egoc. Belcheri, Wright, from the Angulatus bed, may be an example of this species. It exhibits the squared or quadragonal form of this series, and is not, as figured, at all similar to any species of the first subseries. Egoc. intermedium, Wright, from the lower part of the Angulatus bed, probably also belongs to

<sup>1</sup> Quenstedt figures and describes, in his Amm. Schwab. Jura, one old specimen a trifle larger than that described above, which confirms this supposition as to the senile degradation of the keel, and it has no pilæ on the last whorl. The living chamber is still incomplete, though as long as the last volution.

this species. The abdominal view is not similar, not being flat enough on the abdomen, but the lateral view has the straight perfect pile of this subseries.

The Amm. Burguadiæ, Martin, as identified at Semur, is identical with this species. It is, however, smaller than those from Saulieu, which are associated with Psil. planorbe, and is placed in the same bed as Liusicum. Wähner's figures and description of Ariet. Scylla, Reynés, seem to agree closely with the descriptions and figures of this species. The aspect of the umbilical or young whorls in Wähner's figures shows that Scylla, Wäh., is certainly not identical with the Johnstoni-like variety of Cal. raricostatum, though it very closely resembles that form.

#### Caloceras carusense.

#### Plate I. Fig. 15, 16. Plate II. 1-3 a. Summ. Pl. XI. Fig. 15.

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Amm. carusensis, D'Orb., Terr. Jurass. Ceph., pl. lxxxiv. fig. 3-6.

Amm. Arietis, Ziet., Verst. Würt., p. 3, pl. ii. fig. 4 (not fig. 2, 3).

Amm. spiratissimum, Hauer, Ceph. Lias Nordöstl. Alpen, pl. iii. fig. 1-3.2

Amm. latisulcatus longicella, Quenst., Amm. Schwab. Jura, pl. xii. fig. 5 (not fig. 1-4, 6).

Amm. laqueus (pars), Quenst.
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Amm. Scylla (pars), REYNÉS, plates.

 ${\it Localities.} {\it --} {\it Lyme Regis, Semur, St. Thibault, Balingen, Willershausen in Hauover, Luxemburg.}$ 

The characteristic of this species as given by D'Orbigny, the crossing of the abdomen by the pilæ, is not an important peculiarity, since it is common in the young of caloceran forms. The young of the normal variety is, however, identical with D'Orbigny's figure. It acquires the keel when the shell is about 25 mm. in diameter, and is at this stage very similar to one variety of Cal. laqueum. The sides in the later stage and adults become more flattened, and the abdomino-dorsal diameter of the whorl increases proportionally. One variety in the Museum of Comparative Zoölogy has much stouter more quadragonal whorls than this, with flattened sides and abdomen, though the pilæ are never very prominent or perfectly geniculated.

The abdominal lobe is long, and much deeper than the superior laterals. This is owing largely to the non-development of the superior laterals, which remain short and broad. The superior lateral lobes are shallow and broad, the inferior laterals narrow, and not usually long in proportion. The most characteristic parts of the sutures are the first auxiliary saddles; these are remarkably large, and often tongue-shaped. The auxiliaries do not, therefore, incline backwards, at least in adults. The marginal lobes and saddles, and the margins of the superior and inferior lateral saddles and lobes, are simple, and like those of *Psil. planorbe*.

This variety retains the keel until a very late age, even after the shell becomes perfectly smooth. The form at this time is precisely similar to that of the old of the stouter variety of *Cal. Nodotianum* or *tortile*; subsequently, however, the whorl becomes round, as in Plate II. Fig. 1-3 a. This stout variety

<sup>&</sup>lt;sup>1</sup> Mojsis. et Neum., Beitr., VI. pl. xxv.

<sup>&</sup>lt;sup>2</sup> The specimen in Oppel's collection enabled me to quote this as a synonym.

is sometimes identified with Amm. Liasicus in Germany, but that species has a form more like Johnstoni, a larger keel, and entirely distinct sutures.

A specimen from Aldingen, in the Museum of Stuttgardt, shows an entirely smooth senile whorl, precisely similar in form to that described above in the collection of the Museum of Comparative Zoölogy, though it is not half the size, the diameter being 103 mm. Another from Vaihingen had a living chamber still incomplete, though nearly one and a half volutions in length. On the latter part of the eighth volution in this specimen the sides began to become flatter and convergent, and on the ninth and tenth volutions the form was subtrigonal, the channels absent, the pilæ still prominent though obsolescing, and the keel reduced to a raised line; diameter, 163 mm. Another, of nearly the same size as Hauer's figure of Amm. spiratissimum, agreed closely, the sutures also being identical. The form of the whorl is, however, slightly more flattened laterally, It belongs to the large variety of carusense, and is found, according to Hauer. with Conybeari, rotiformis, and bisulcatus, in the "gelben kossener Schichten of A specimen from Elwangen, labelled Amm. torus, in the Geo-Enzesfeld." metricus zone, exhibits all the characteristics of the large specimen described above. It has larger and stouter whorls and pilæ than the specimens described from the Lower Bucklandi beds, though the sutures and other characteristics are similar. A specimen of this variety from Aalen also occurs in Professor Quenstedt's collection at Tübingen, with larger and more prominent pilæ than usual.

The young and old stages of this species at Semur and elsewhere are usually identified either as *torus*, or *tortilis*, or *Johnstoni*, because of the resemblances of the stages of development and senility in the different species of this series.

# Caloceras longidomum, HYATT.

Amm. longidomus, Quenst., Amm. Schwab. Jura, p. 50, pl. vi. fig. 1, 2. Amm. longidomus æger, Quenst., Ibid., pl. vi. fig. 3.

This species, as described and figured by Quenstedt, cannot be classified with certainty. Not having seen specimens unquestionably referable to the species, we cannot positively decide as to its true affinity. It is, according to Quenstedt's description, a more immature or primitive form than spiratissimum, since he alludes emphatically to the resemblances between the young and Psiloceras. He also states that the young are closely allied to the young of spiratissimum. This evidence seems to conflict, but the sutures, their backward inclination, and the fact that the abdominal lobe, though longer than the superior laterals, is only slightly longer, the not very prominent and curved pilæ of Quenstedt's figure, the broad keel and slight channels, and the somewhat compressed form of the older whorls, are all characteristics similar to those of carusense. It may be a variety of carusense larger than the French, and becoming senile more slowly. The curved pilæ are not like laqueum, and the cylindrical whorl and tendency of the pilæ to cross the abdomen in the young also suggest connection with carusense.

#### Caloceras Nodotianum, HYATT.

Plate I. Fig. 7-11 a. Summ. Pl. XI. Fig. 16.

Amm. Nodotianus, D'Orb., Terr. Jurass. Ceph., p. 198, pl. xlvii.

Locality. - Semur.

I have never seen the original, but the species as identified in D'Orbigny's collection and at the Museum of Semur, and also in Boucault's collection named after D'Orbigny's types, has not a close resemblance to Oppel's type of Nodotianum. This last is probably its morphological equivalent in the genus Arnioceras, since it has smooth young, and is otherwise similar to Arnioceras. A specimen in the Museum of Comparative Zoölogy, said to be from Semur, has a stouter form and straighter pilæ than any specimen I have seen elsewhere. It has in these characters and in general aspect resemblances with forms like Cal. proaries, var. latecarinalum, but the abdomen differs in not being so much flattened.

The fine suite of specimens in the Museum at Semur shows that this species has several varieties. One resembles the variety of Cal. tortile from Waldenburg. Another, at 128 mm. diameter, has the sides inclined and the abdomen narrow, but not yet entirely acute. Another, even at the small diameter of 57 mm., has an abdomen acute, as is represented in D'Orbigny's figure. The septal digitations of this species are not so complicated as in Liasicum or the torus variety of Johnstoni. The examination of the specimens in the Museum at Semur shows them to have been derived from Cal. carusense. The shells found in the Tuberculatus bed resemble the adults of this species until a late stage of growth. Plate I. Fig. 11, represents the full-grown adult, and Fig. 11 a section of the last whorl with its broad abdomen; Fig. 7, a larger specimen; Fig. 9, 10, the approach of old age in a fragment of a still larger specimen. In the section the abdomen is shown growing narrower on the last whorl.

### Caloceras raricostatum, HYATT.

# VAR. A.

# Plate VI. Fig. 15.

Amm. raricostatus, D'Orb., Terr. Jurass. Ceph., p. 212, pl. liv. fig. 1, 2 (fig. 3, var. B).
Amm. raricostatus, Quenst., Amm. Schwab. Jura, pl. xxiii. fig. 22, 23; pl. xxiv. fig. 4-10 (other figs., var. B).
Ariet. raricostatus, Wright, Lias Amm., pl. vii. fig. 2-6 (pl. xxvi. fig. 5-14, var. B).
Ophioceras Johnstoni, Hyatt, Bull. Mus. Comp. Zoöl., I., No. 5, p. 75.

 ${\it Localities.} - {\it Lyme Regis, Somerset, St. Thibault, Semur, Salins, Balingen, Boll, Willershausen in Hanover.}$ 

The pilæ apparently begin abruptly, but they are really preceded by depressed folds hardly perceptible to the naked eye. The pilæ are very closely set at first, but begin to be more widely separated on the fifth or sixth whorl. On the third or fourth whorl there are over forty, while on the eighth whorl there are not over thirty. No other changes take place in them or in the

form of the whorl until about the sixth whorl. During this volution the abdominal region is raised to a slightly greater prominence, and the siphonal ridge appears.

A large specimen from Semur shows pilæ, which are obtuse, but prominent and bent forward. These characteristics belong to the adult stage, and are preserved without change throughout the tenth whorl. On the ninth and tenth volutions the pilæ are very numerous, being respectively forty-one and thirty-eight in number, and the young of this shell must have had a larger number of pilæ than any specimens described above. On the second and third quarters of the eleventh volution the pilæ became more and more depressed, and finally disappeared. The twelfth whorl was rounded and smooth, like that of the young, and therefore a good illustration of the nostologic stage.

There is not usually much variation in the sutures of this species. The abdominal lobe is considerably longer than the superior lateral lobes, and the inferior laterals may be of about the same length, or not more than half as long. The superior lateral lobes are broad at the summits and serrated, the inferior lateral lobes are very small in some specimens, owing to the small size of the first auxiliary saddles. The two larger saddles may be of equal depth, or the inferior laterals somewhat the deeper; the superior laterals are, however, very broad in proportion to their depth, and the inferior laterals much narrower, occasionally even club-shaped. These proportions are apparent at an early age, and were observed upon the latter part of the third whorl before the development of the marginal lobes.

#### VAR. B.

# Plate I. Fig. 24, 25 a.

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    Amm. raricostatus, Ziet., Verst. Würt., p. 18, pl. xiii, fig. 4.
    Amm. raricostatus, Quenst., Amm. Schwab. Jura, pl. xxiii. fig. 8-21, 24-31; pl. xxiv. fig. 1-3 (other figs., var. A).
    Amm. raricostatus, Hauer, Ceph. Lias Nordöstl. Alpen, pl. xvi. fig. 10-12.
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Ariet. raricostatus, WRIGHT, Lias Amm., pl. xxvi. fig. 5-14 (pl. vii. fig. 2-6, var. A).

Ophioc. raricostatus, HYATT, Bull. Mus. Comp. Zool., I., No. 5, p. 75.

The true pilæ begin upon the third whorl. There are about forty on the third and fourth whorls, decreasing to about twenty-five on the fifth whorl, and on the seventh whorl there are only about twenty pilæ, the last of which already begin to exhibit symptoms of senile degradation. On the eighth whorl the pilæ are degraded to mere blunt folds. The remainder of this whorl could not be observed, but a fragment of the first quarter of the ninth shows that these blunted folds are still more depressed, being merely lateral ridges. The whorl at this time has an elevated abdomen, and the keel has disappeared. The form is similar to the old age of the stout variety of *Cal. tortile*.

The distinctions between this and the preceding variety are to be sought in the sutures, the development of the pilæ, and the size of the adult shell. The young are precisely like the young of Cal. carusense, Amm. arietis, Ziet., but on the fifth volution the whorl spreads out more laterally, and the pilæ

become more prominent as well as more widely separated and fewer in number than on the fifth whorl of this species or of *Cul. Johnstoni*.<sup>1</sup>

The large form of *Cal. carusense* exhibits no sign of senility on the beginning of the ninth whorl, thus attaining a much larger size in its adult condition than the typical *raricostatus*, which often exhibits signs of senile decay upon the latter part of the seventh whorl.

The abdominal lobe is somewhat longer than the superior laterals, and the inferior laterals shorter than, or about equal to, the superior laterals. The superior lateral saddles are very broad in proportion to their depth, as are also the inferior laterals, the latter being either equal to or rather deeper than the former. The first auxiliary saddles are, as usual, very variable in size and form, but when compared with the inferior laterals they are very much more prominent than in the adult of Cal. carusense. This seems to be the only marked difference between the sutures of these two species, and it is probably not very important.

The true raricostatus from the Raricostatus bed, is rarely misnamed in collections, but there are other forms of distinct species occurring earlier which are frequently misnamed raricostatum. The peculiar variety of tortile from Quedlinburg is one of these, but it has smooth and gibbous young whorls like the young of Johnstoni. Cal. sulcatum, with coarse but sparse pilæ, from Semur, is another example. Some varieties of carusense afford other examples, but raricostatus is frequently almost inseparable from the young of carusense until the specimens are over 51 mm. in diameter.

The adult of variety A of true raricostatum is almost precisely like carusense in those varieties which have very closely set pilæ in the young, as in Plate I. Fig. 16. Cal. raricostatum, var. A, therefore, seems to have arisen through an arrested development of carusense, and then subsequently to have given rise to the peculiar flattened typical whorls of variety B.

#### Caloceras aplanatum, HYATT.

Ariet. tardecrescens, Blake, Yorkshire Lias, p. 285, pl. v. fig. 5 a, b. Locality. -- Whitby.

This species is represented by a specimen which we were at a loss to dispose of until we read Blake's description, and saw the figure. The latter is poor, but with the description it suffices, if one has a specimen in hand. The whorl in the young has a completely caloceran form and pilæ, which are similar to the young of Cal. raricostatum. It is in fact a much compressed, keeled, channelled form of caloceras similar to Nodotianum. It occurs in Blake's Jamesoni bed of the Middle Lias, but is doubtless to be accounted for in the Raricostatus bed of Wright, which is included in Blake's Jamesoni bed. It is discoidal, and the pilæ on the outer whorl have become depressed and curved. Specimens in the British Museum from Robin Hood's Bay have been named Conybeari by

<sup>&</sup>lt;sup>1</sup> Plate I. Fig. 25 a represents an abdominal view of the adult.

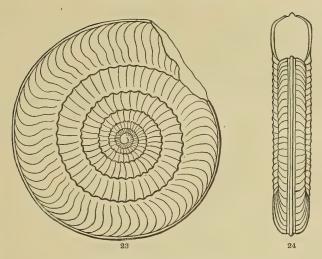


Fig. 23, 24. Views from the side and abdomen of Cal. aplanatum.

Bean, and were said to have been found in the Lower Lias. Their young, seen from the side and only in the umbilicus, have the peculiar pilæ and general aspect of *raricostatus*, with similar rotund sides and fine closely set pilæ.

Cal. (Ariet.) præspiratissimum, Wäh., has distinctly caloceran sutures and pilæ without geniculæ. It develops a keel at an early stage, and has a subquadragonal whorl in the adult with slight channels. It is a close morphological equivalent of the Vermiceran-like variety of Cal. laqueum of Central Europe, if not identical with it, and is certainly, as stated by Wähner, transitional to Ver. spiratissimum.

Wähner's figures prove that Cal. proaries is a form with late development of a keel, the exact equivalent of Cal. Nodotianum in the Central European province. Wähner's full series of young and adults, and Neumayr's senile specimen figured in Unterster Lias, show that the young of Cal. proaries (Plate XXX. Fig. 7) resemble very closely the adult stages of Psil. sublaqueum, Wäh. (Plate XXX. Fig. 4), Cal. Johnstoni (Plate XVI.), and Cal. (Psil.) orthoptychum, Wäh. (Plate XXVII. Fig. 2), and the unnamed form figured on Plate XXVII. Fig. 3. Cal. (Psil.) gonioptychum, Wäh., has the same compressed whorls as in the more advanced stages of proaries, and appears to be intermediate between that species and Cal. cycloides. The sutures agree with those of proaries. We venture to differ from Wähner, who associates this species more closely with Cal. Sebanum of the Planorbis bed. The apparently intermediate aspect and characteristics seem to have been inherited at an earlier stage than in proaries, but not quite so early as in cycloides, if one can use figures for arriving at such conclusions. Cal. (Ariet.)

<sup>&</sup>lt;sup>1</sup> Mojsis, et Neum., Beitr., V. pl. xxi.

<sup>&</sup>lt;sup>3</sup> Abhandl. geol. Reichsans., VII. pl. xxviii.

<sup>&</sup>lt;sup>2</sup> Ibid., IV. pl. xxviii.-xxx.

<sup>4</sup> Mojsis. et Neum., Beitr., IV. pl. xxvii.

eycloides, Wäh., is a slightly more compressed form, which may be transitional between the last and the next species, Cal. (Ariet.) Doetzkirchneri. This last is figured by Neumayr. Wähner's figures of the young of this species show the rounded sides, slight keel, and pilæ similar to those which proaries has at later stages in some specimens, and even in adult stages in others. Cal. (Ariet.) Castagnolai, figured by Wähner, shows in its very compressed whorls, narrower umbilici, and sharp prominent keel, which are well developed at an early stage, when the shell is about 15 mm. in diameter, that the cycle of normal modifications is approaching completion. Cal. (Ariet.) abnormilobatum gives us the final gradation. This is a shell having still more compressed whorls, narrower umbilici, due to the more involute whorls, and a more attenuated keel.

This keel and that of Castagnolai leads to the suspicion that it may be hollow, but Wähner is too keen an observer, as shown in his complete descriptions, to have let such an obvious peculiarity pass unnoticed. His remarks also show that he knows how to distinguish between the morphological equivalence of this species with Oxynoticeras and its true genetic affinities, as demonstrated by the nealogic stages and their similarities to the later stages and adults of Castagnolai and cycloides. Wähner's descriptions, which we did not consult until we had written the above, are sustained by our experience so far as the serial relations and affinities of Doetzkirchneri, cycloides, Castagnolai, and abnormilobatum are concerned.<sup>5</sup>

### THIRD SUBSERIES.

This subseries contains species which have better defined channels and more prominent keels in the adults than is common in the second series, and during the clinologic stage these are still retained. The whorl in other words becomes rounded only in the nostologic stages, and probably very rarely attains this extreme of modification. The clinologic stage has also slightly flattened and inclined sides.

### Caloceras sulcatum, HYATT.

Plate I. Fig. 19, 20. Summ. Pl. XI. Fig. 20.

Amm. Conybeari, Ziet., Verst. Würt., pp. 3, 35, pl. ii. fig. 4?
Amm. Nodotianus, Hauer, Ceph. Lias Nordöstl. Alpen, pl. vi. fig. 4?
Amm. kridion, Quenst., Amm. Schwab. Jura, pl. ii. fig. 7 (not fig. 5, 6).

Locality. - Semur.

This species is precisely similar to Hauer's figure, except that the sutures are more distinctly caloceran, having the line of auxiliaries inclined backwards. Our specimens are also somewhat stouter, the abdomen broader, the channels deeper, the geniculæ more prominent, but the pilæ and general aspect of the shell are exactly similar.

- <sup>1</sup> Mojsis. et Neum., Beitr., V. pl. xxii., xxiii.
- Abhandl, geol. Reichsans., VII. pl. v. fig. 1.
   Mojsis. et Neum., Beitr., V. pl. xxii., xxiii.
   Ibid., pl. xxviii. fig. 4-7.
- <sup>5</sup> We have given outline figures on Summ. Pl. xi. of Cal. cycloides, fig. 17, Castagnolai, fig. 18, and abnormilobatum, fig. 19.

One specimen in the Museum of Comparative Zoölogy has somewhat deeper channels than is usual in this species, but is otherwise quite similar to the raricostatus-like variety (Plate I. Fig. 19, 20). Quenstedt identifies this variety with Arn. kridioides (kridion) in his "Ammoniten der Schwabischen Jura," but from this species it differs essentially, if we are right in our selection of the form to which the name Amn. kridion, Oppel, has been applied. Undoubtedly there is a close resemblance between this species and raricostatum, on the one hand, and Arn. kridioides on the other. The young and the channels separate it from the former, and the great breadth of the whorls, channels, caloceran pilæ, and sutures, from the latter. The raricostatus-like form of the whorl and pilæ, and absence of tubercles, distinguish it from what we consider to be the true kridion. Zieten's figure of a specimen from Kalthenthal, near Stuttgardt, has exactly the aspect of this species, and though the abdomen looks somewhat broader in Zieten's section the pilæ have no tubercles. It is more like this species than any form of kridion or kridioides, if the figure is accurate.

# Caloceras laqueoides, HYATT.

Amm. sinemuriense, FRAAS.

In this specimen, now in the collection of the Museum at Stuttgardt, found, according to Fraas, in the Angulatus bed, there is a most singular mingling of the characteristics of *laqueum* with the peculiar pilæ of *Coroniceras Bucklandi*, var. sinemuriense.

The young and adult whorls are smaller and more numerous than those of sinemuriense, and like those of laqueum. The abdomen, however, has narrow channels, and many of the pilæ in the adult have large tubercles somewhat thrown back, which give them the aspect of the undivided pilæ of sinemuriense. Between these there are usually two or more of the linear pilæ of one variety of laqueum, and the tubercles when covered by the shell do not extend into spines, but remain mere tubercles.

In old age or on the last whorl of this specimen, which may perhaps be prematurely old, the intermediate pilæ alone are found, the stout tuberculated simuriense-like pilæ having become obsolescent. At this time the form and characteristics of the whorl are precisely as in laqueum, except the channels; these still remain very much shallower. Upon the whole, therefore, it is probable that this may be a distinct species. Together with others, it shows that Caloceras may have forms which are the morphological equivalents of the tuberculated, keeled, and channelled progressive forms of Vermiceras, Coroniceras, and Asteroceras.

### Caloceras? Deffneri.

Summ. Pl. XI. Fig. 21.

Amm. Defineri, Opp., Mittheilungen, II. p. 131, pl. xl.

Locality. — Stuttgardt.

This species has whorls at first sight apparently identical in form with those of the typical Conybeari.

The young have prominent pilæ and geniculæ on what seems to be the first quarter of the fourth whorl, and the geniculæ become tuberculated in the adult, without, however, exhibiting the angular forward bend of *Compbeari*.

The abdominal lobe is extremely broad, its lateral branches at first extending over the channel ridges on either side, and then diminishing to two pointed minor lobes. The siphonal saddle is very large. The superior lateral lobes are very narrow, profusely branching, a trifle longer than the abdominal lobe, and very much longer than the inferior laterals. These and the auxiliary lobes are often inclined posteriorly, as in Caloceras. The inferior lateral saddles are about as deep as the superior laterals, and have deeply cut margins, as in that genus. The first auxiliary, however, is often of considerable size, and then the inclined aspect of the inner margin is destroyed. The superior lateral saddles are penetrated by a very peculiar and remarkable marginal lobe, which divides them into two portions, the inner shorter than the outer half. The proportions of the lobes and saddles, and this last peculiarity, show, besides the form, a closer repetition of the characteristics of *Conybeari* than could have been anticipated from the general aspect of the shells.

The channels are shallow, but have lateral ridges, and the keel is well formed and prominent, as in *Conybeari*. The series of this species in the Museum at Stuttgardt illustrates the different ages at which senile characteristics may begin to appear. The last specimen described above was only 175 mm. in diameter. Another specimen, however, reached the size of 380 mm., and yet only the last volution and a half exhibited senile degradation. The first senile half-volution had obsolescing pilæ and tubercles, while the last half-volution was entirely smooth. The channels and keel remained almost unchanged, as in the adult. Not even a fragment of a living chamber was present. Oppel's original is in the Museum at Stuttgardt. The eighth and ninth whorls of this specimen are senile, the tubercles have disappeared, the sides are more convergent, and the abdomen more elevated than in the adult; the keel and channels, however, were retained even after the pilæ disappeared, though they had become shallower.

The sutures indicate affinity with the Caloceran series, but our knowledge of the early stages is incomplete, and this opinion is consequently uncertain.

Neumayr in his "Unterster Lias" figures a large specimen of Cal. (Ariet.) Haueri, and gives a section. These show that the nealogic stages of this species are first similar to Johnstoni, then as the keel appears resemble Cal. Loki and the like, and finally take on the narrow channels of the adult. The closely set, bent,

immature-looking pilæ are also characteristic and persistent in this subseries. The sutures are distinctly caloceran. Our own notes made in the Museum at Munich give the same results as regards this important species. clearly points them out as transitional, while calling the species an Arietites. It is evident that we differ mostly in the limits which are ascribed to genera. Cal. (Ariet.) Loki, Wäh., and Cal. (Ariet.) Seebachi, figured on Plate XX., indicate, when compared with Cal. (Ariet.) Haueri, Wäh., that Haueri must have been connected with Johnstoni through some such flat-sided shells as the former. The Cal. (Ariet.) Haueri of Wähner, as figured on Plate XIX. and especially on Plate XVII., shows acceleration in the earlier development of the keel and channels. The specimen on Plate XVI. Fig. 3, though about the size of the specimen figured on Plate XVII., has very shallow channels, and an immature keel, which contrast markedly with the deep channels and perfect keel of the former. Cal. (Ariet.) coregonense, Wäh.,2 is figured so fully that, as in Cal. Haueri, one can see that the keel and channels were developed at different stages of growth, in some much earlier than in others, and that old age began also in some cases much earlier than in others. Cal. (Ariet.) ophioides,3 Wäh. (not D'Orbigny's species, which is a true Vermiceran species with constant channels, tuberculated pilæ, etc.), has also varieties in which channels are very late in appearing, and others in which they appear early. Cal. (Arict.) perspiratus, Wäh., a stout form of whorl, but the age at which channels appear is not given. Cal. (Ariet.) supraspiratus, Wäh.,5 has the channels developed at an early age as compared with other species.

### Caloceras Newberryi, 6 HYATT.

Locality. - Peru.

Two very interesting specimens of this species have been placed in my hands for identification and description through the kindness of Prof. J. S. Newberry. They are reported as having been collected near, but not at, the Cerro de Parco mines in Peru. The largest is 128 mm. in diameter; abdomino-dorsal breadth of last whorl, 24 mm.; transverse diameter, 20 mm.; next inner whorl, 20 by 16.5 mm. It resembles the form of Cal. Nodotianum in the aspect of the section when restored, and in the number, close proximity, and linear appearance of the pilations. They are also similar in being slightly and evenly curved. The keel is low and broad, the channels shallow and more distinct than in the figure, but the abdomen similar to that of the section, Fig. 9, Plate I. The outer whorl of the older stages and all the inner whorls are compressed, as in the typical forms of Nodotianum. The distinct keel and shallow channels appear late in the life of the shell, as is usual in that species. The living chamber is incomplete, but over one volution in length. The species more closely resembles Cal. proaries, Neum., than any other form of the fauna of the Northeastern Alps, but differs in having flatter sides in all the whorls, an earlier

Mojsis, et Neum., Beitr., V. pl. xvii.
 Ibid., VI. pl. xxi.—xxvi.
 Ibid., pl. xx.
 Ibid., pl. xx. fig. 6-9.
 This species has been referred to previously in these pages as if identical with Cal. Nodotianum.

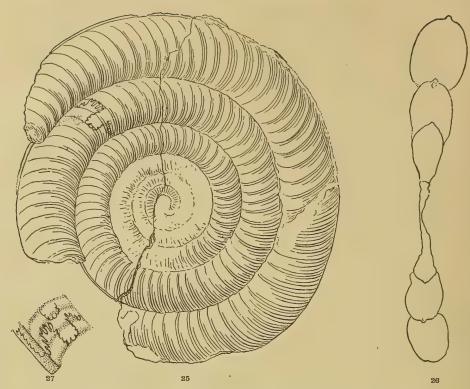


Fig. 25, 26. Views from the side and in section of Cal. Newberryi showing incomplete living chamber and outlines of whorls.

Fig. 27. View of suture made up from the last suture in Fig. 23 and the study of others. The abdomen is projected, to show depth and narrowness of abdominal lobe.

development of keel and channels, narrower abdomen in the whorls of the adult, and in being, like the species of Central Europe, considerably smaller. The largest specimen had just begun to pass into the first senile stage. The internal or young whorls have pilæ similar to those of the young of Cal. raricostatum and Cal. carusense. The sutures are similar to those of the normal species of Central Europe, having broader lobes and saddles than is customary in the basin of the Northeastern Alps. This agrees with other characteristics, which are essentially similar to species from the European province. The second and smaller specimen, which is 80.5 mm. in diameter, has similar but straighter pilæ. The abdomen is broader and more depressed, and the channels better defined, but how much of this is due to pressure cannot be stated. Both specimens have been distorted by pressure. The first has been affected in such a way that it is easy to restore the normal form, whereas in the second case it is not easy to separate the results of pressure from the true characters.



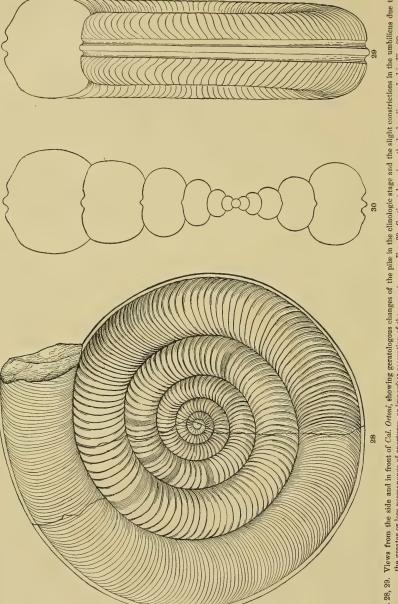


Fig. 28, 29. Views from the side and in front of Cal. Orion, showing geratologous changes of the piles in the clinologic stage and the slight constrictions in the umbilicus due to the greater or less permanence of apertures, or imperfect resorption of these apertures.—Fig. 30. Section taken along the broken line marked in Fig. 28.

### Caloceras Ortoni, HYATT.

Caloceras Ortoni, Нуатт, Proc. Bost. Soc. Nat. Hist., XVII., p. 367.
Locality. — Tingo, near Chacapoyas, Northern Peru.

The shell is fully preserved in the only specimen found. This form resembles Cal. salinarium of the Northeastern Alps more than any other species. There are the same closely crowded fold-like bent pilæ without geniculæ, similar narrow channels with depressed lateral ridges and sunken keel, and similar gibbous form of whorl, flattened abdomen, and discoidal aspect. The young were studied in section. The earlier stages are excessively broad and smooth for three whorls. Coarse tubercular folds appear on the latter part of the third or first quarter of the fourth volution, near the abdomen. These gradually lengthen, but remain very broad folds separated by wide depressions during the entire fourth whorl. There are about twenty pilæ on this whorl including the tubercles, thirty-five on the fifth, and perhaps fifty-eight on the sixth.

Occasionally a pilation is wanting, indicating the former presence of a more or less constricted aperture, but these, though numerous, are not at regular intervals. Occasionally pilations are doubled, but these are not shown in the figure.

On the seventh whorl there are about eighty pilæ, and on the latter part of this volution they begin to lose their prominence, and on the latter part of the eighth they suddenly degenerate into coarse crowded striations. These changes are accompanied by a very slight elevation of the abdomen, broadening and shallowing of the channels, while the keel appears to be more prominent.

The young whorls are similar to those of *Cal. Liasicum*. The keel appears as a low, broad ridge on the first quarter of the sixth volution, but the channels were not present, in the section examined, until first quarter of seventh volution. They are at this time very shallow and narrow, and the keel is also depressed and not very broad, but on the eighth volution both these parts become more fully developed. Effort was made by removing the shell to see the sutures, but not with success. The auxiliary portions of the sutures are inclined posteriorly, but otherwise nothing was satisfactorily ascertained.

Cal. (Ariet. proaries var.) latecarinatum, Wähner, is the geographical equivalent of the broad, depressed-whorled varieties of Cal. Liasicum of the Middle European province. Wähner considers that Loki may be the nearest affine to Cal. Liasicum, taking as his guide Reynés's figure of the latter. This means only the compressed varieties of this species, which we have noted in the first subseries. The extreme depressed whorls of latecarinatum are closely similar to the next form of the subseries Cal. (Ariet.) salinarium, figured on Plate XVIII., and this is very likely, as supposed by Wähner, an old specimen of salinarius, though described by Gümbel as Amm. euceras. Cal. (Ariet.) centauroides, Wäh., exhibits very stout whorls in the young, and acquires the deep channels and well developed keel at a late stage of growth, and these continue to be better

<sup>&</sup>lt;sup>1</sup> Mojsis, et Neum., Beitr., V. pl. xvi.

defined, though the first old age stage is shown to have begun by the flatness and inclination of the sides in the section given by Wähner on Plate XXIV. Fig. 7 e. Cul. (Ariet.) Grunowi (Hauer), Wäh, 1 resembles closely centauroides, but is evidently even less advanced, since the development of the keel is less marked, and it is doubtful if it ever have channels. The two species mentioned above, centauroides and Grunowi, as described by Wähner in their younger stages, have sutures which differ from the similar forms described by Canavari in his Fauna of the Lias, so often quoted above. The sutures are unquestionably arietian, having deep narrow abdominal lobes and lateral sutures like those common in Caloceras. The sutures, form, and characteristics of Aegoc. centauroides, Canavari, figured on Plate V., ally it closely with the species figured on Plate VII. as Aegoc. Listeri.<sup>2</sup>

The extraordinary species figured by Neumayr, Cul. (Egoc.) Sebanum, Pich.,<sup>3</sup> is supposed by him to be a species with young, like those of the schlotheimian series. It is apparently, if the figures are accurate, a keeled caloceran form, with prominent angular geniculæ in the young, and we entirely agree with Wähner that it cannot be allied to Schlotheimia. Such a shell might be traced either to Cal. tortile, or almost any species of Caloceras having an immature keel and well defined pilæ. The characteristics suggest a subseries of which the tuberculated Cal. laqueoides of the Angulatus bed of Würtemburg would be also a member.

Geyer, in his "Lias. Ceph. d. Hierlatz b. Hallstadt," gives three species of small size, Cal. (Arietites) sp. indet. aff. Nodotianus, D'Orb., Plate III. Fig. 16; Cal. (Ariet.) doricus, Plate III. Fig. 3; and Cal. (Ariet.) raricostatus. This is a fauna mostly composed of dwarfed forms of species, which there lived under unfavorable conditions, as did those of Spezia in the south.

Canavari, in his Unteren Lias v. Spezia, gives Cal. (Ariet.) Corregonesse, Fig. 12–15, which seems to be the young of a stout variety of Johnstoni; Cal. (Ariet.) retroversicostatus, which may be young of Cal. salinarium described by Wähner from the Northeastern Alps; Cal. (Ægoc.) helicoideum, Plate V. Fig. 7, tortuosus, Fig. 8, and carusense, Fig. 10, all belonging apparently to the same species, most likely young or dwarfs of the last named; 4 and Cal. (Ariet.) raricostatum, Fig. 9, is probably the young of some Caloceran species, since the drawing does not have the aspect of raricostatum.

#### VERMICERAS.

In this genus we find several characteristics which were merely specific or varietal in Caloceras, becoming established as an integral part of the growth, and furnishing good generic characteristics.

<sup>1</sup> Mojsis. et Neum., Beitr., VI. pl. xxv. fig. 2, 3.

Unterst. Lias, Abhandl. geol. Reichsans., VII. pl. iv. fig. 2-4.

4 Referred by Canavari to the young of proaries in Mem. della Carta Geol. d' Italia.

<sup>&</sup>lt;sup>2</sup> The species accompanying this one, figured on the same plate as *Tropites ultratriasicus*, *Arietites Campigliensis*, *liqusticus*, and *discretus*, are all apparently true Tropites with tuberculated and coronate whorls in the earlier nealogic stage, and acquiring a keel and pilæ while still retaining the coronate depressed form of their triassic radical, *Tropites subbullatus*. The sutures as figured are similar to those of the adult of *Tropites Jokeyli*, as given by Hauer, Ceph. d. Hälst. Schich., Denks. Akad. Wien, IX., 1855, pl. iv.

The young whorls for a very limited stage are smooth, then the rounded abdomen and immature pile of Caloceras appear. The keel is introduced after this stage, and we have for a stage of greater or less duration, according to the species, a resemblance to some varieties of *Caloceras laqueum*.

The adults are characterized by quadragonal forms and flattened, keeled, and channelled abdomens. The pilæ are straight, with distinct geniculæ bending forwards. In one variety of *Verm. Conybeari* the geniculæ are tuberculated, in other examples they are smooth.

The sutures have arietian proportions in the adults, though they retain the immature proportions of the young until a late period of growth, and often even in the adult stage. The abdominal lobe is longer than the superior laterals, and the superior lateral saddles shallower than the inferior laterals; the auxiliary saddles and lobes may occasionally have a backward trend in the young, but this is not found in adults.

The old stage retains the keel, and has smooth, somewhat flattened and convergent sides. This is very distinct from the similar stages of Caloceras, in which the keel is lost and the whorl becomes rounded. The extreme form assumed in old age, when contrasted with the adult whorl, can be best described as trigonal. It is, however, still similar to the senile stages of Caloceras before the keel is lost, and the sides are more gibbous than in the trigonal senile whorls of the more highly developed species of Coroniceras. The sutures degenerate, the abdominal lobe becomes shorter. Our observations on the geratologous period in this genus were not so satisfactory as in some others, senile specimens being of rarer occurrence. Quenstedt, in his "Amm. Schwab. Jura," Plate VII., figures under the names of brevidorsalis and brevidorsalis macer several fragments of large shells, which are probably examples of senile metamorphoses belonging to this genus, but we are not able to designate the probable species. Although the last whorls are represented as perfectly smooth in these figures and the sides convergent, and the abdomen considerably narrowed, the keel and channels are still persistent. The whorl in the oldest specimen had become so excessively altered by senile degradation that it was smooth and helmet-shaped, as in Psiloceras, and the channels obsolescent, though a low broad keel still remained.

There is also in the British Museum a fossil, 1010 mm. in diameter, labelled, "Zone of A. planorbis and Pent. tuberculatus, Newbold Quarries, Rugby, Warwickshire." This has the outer whorls compressed and smooth, as in Psil. planorbe, but with a keel and obsolescent channels preserved on part of the last volution. We identified this as an aged specimen of Verm. Conybeari, but eminent paleontologists in England have expressed their opinion that it might be a specimen of planorbe. We are much indebted to Mr. Henry Woodward, of the British Museum, for a large drawing of this fossil, but unfortunately this is not sufficient to settle the questions involved. We have had no opportunity for re-examination, and should have considered our former opinion as probably erroneous but for other evidence. According to Wright, Pentacrinus tuberculatus is not found below the Angulatus bed in England. We have also seen in the rock at Lyme Regis sections of old whorls of Conybeari closely resembling this, and also a still more advanced stage,

in which the channels were entirely obsolete, the keel being almost completely merged in the surface, or represented only by a raised sub-angular line on the sub-acute abdomen.

These specimens are among the few rare examples of species in this family which have entered upon what we have called the nostologic stage on account of the resemblances to ancestral forms which make their appearance in consequence of senile degeneration of the differential characters of the preceding adult stages. It is to be anticipated that in very exceptional cases of extreme senility, the reversion to the form and characteristics of *Psil. planorbe* may have been completed by the entire loss of the keel at the termination of the nostologic stage, but we have not yet seen such a case in Vermiceras, or any other keeled and channelled genus of the normal Arietidæ.

## Vermiceras spiratissimum, HYATT.

Plate I. Fig. 17, 18. Summ. Pl. XI. Fig. 23.

Amm. spiratissimus, QUENST., Handb. d. Petrefact., p. 355, pl. xxvii. fig. 9; Amm. Schwab. Jura, pl. xii. fig. 7-10; pl. xiii. fig. 1, 2, 6.

Discoceras spiratissimus, HYATT, Bull. Mus. Comp. Zool., I., No. 5, p. 77.

Amm. arietis, ZIET., Verst. Würt., p. 3, pl. ii. fig. 2, 3 (not fig. 41).

Amm. Conybeari, Ziet., Ibid., p. 35, pl. xxvi. fig. 2.

Amm. latisulcatus, QUENST., Amm. Schwab. Jura, pl. xii. fig. 1-4 (not fig. 5, 6).

Localities.—Whitby, Semur, Filder, Stuttgardt, Balingen, Vaihingen, Nellingen, Metzingen, Hohenheim.

Var. A. The pilæ begin early upon the third whorl, the shell during the first two whorls being smooth. The pilæ are about twenty in number on the third or fourth whorl, and increase to from thirty-two to thirty-four on the sixth whorl, and forty-five to fifty on the eighth. The aspect of the shell, until the keel becomes well defined, is precisely like that of the adult of Cal. laqueum. At earlier periods the development is the same as in that species; the keel, however, is always developed earlier. The whorls assume the flattened sides and abdomen on the fourth whorl, and this continues in some specimens throughout the fifth. The channels become deeper upon the last quarter of the fifth whorl or the first quarter of the sixth; but while these remain without well defined lateral ridges, the shell continues immature. When, however, the ridges appear, the abdomen and the pilæ gradually acquire their adult characteristics.

The variety figured on Plate I. Fig. 18, might be called the dwarfed or raricostatus variety of this species. The pilæ are between fifteen and nineteen in number on the third whorl, and only about twenty-two on the fourth, increasing again to twenty-six on the fifth. The young, however, are like those of typical spiratissimum.

Senile characters made their appearance in one specimen upon the ninth whorl. A fragment of the fourth quarter of this whorl, in one specimen, exhibited unmistakable signs of advanced senility. The pilæ are only ridges, destitute of geniculæ and slightly bent forwards. The whorl is broader near the dorsum, and the sides converge. The keel and channels remain apparently unchanged.

<sup>&</sup>lt;sup>1</sup> This seems to be identical with carusense, judging from the type in Oppel's collection.

The sutures have reverted to larval outlines. On the eighth whorl the lobes are all of equal length; the superior lateral saddles, however, are deeper than the inferior laterals, and the first auxiliary saddles not more than half as deep as the inferior laterals.

The abdominal lobe and the larger saddles are much shallower in proportion to their breadth in this species than in *Conybeari*. The rate of increase in the bulk of the whorl by growth is also less than in *Conybeari*, and the umbilicus shallower. The longest living chamber was observed in a specimen in the Museum of Stuttgardt from Vaihingen; it was full one and a half volutions in length, and not complete. Quenstedt figures a senile specimen with a living chamber, the aperture preserved, which is a trifle over one and a half volutions in length. The aperture is remarkable for having no lateral sulcations, and no abdominal rostrum. It would be instructive to compare this with the aperture of an adult or young specimen, since it suggests degeneration in the rostrum, and, if this be true, is another characteristic occurring through senile metamorphosis which is analogous to the younger stages.

The Museum of Comparative Zoölogy received in exchange from the Museum of Stuttgardt a young specimen of this species labelled "Anm. laqueus, Quenst., Lias, and found with Anm. psilonotus at Nellingen." The geniculæ had already begun to be developed, and the presence of a subquadragonal form of whorl, as well as the keel and immature channels, at such an early age, shows that this must have been a vermiceran and not a caloceran species.<sup>3</sup>

A specimen from the Arietenkalk in the Museum of Tübingen, and belonging either to this or to *Cal. longidomus*, has a rupture in the shell at an early age, and is distorted. The distortion of the spiral is slight, but the pilæ cross the abdomen, which has no keel. On the first part of the exposed whorl they are more or less alternate, but subsequently quite regular, and on the latter part of this whorl a keel-like ridge appears below, though not high enough to interrupt the pilæ. The diameter of this specimen is about 39 mm.

#### Vermiceras Conybeari, HYATT.

Summ. Pl. XI. Fig. 24.

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Amm. Conybeari, Sow., Min. Conch., I. p. 70, pl. cxxxi.

" " D'Orb., Terr. Jurass. Ceph., p. 202, pl. l.

" " Quenst., Amm. Schwab. Jura, pl. xv. fig. 1.

" " Haufr, Ceph. d. Nordöstl. Alpen, p. 16, pl. ii. fig. 1-6.

Discoc. Conybeari, L. Agassiz, Bull. Mus. Comp. Zoöl., I. No. 5, p. 77.

Ariet. Conybeari, Wright, Lias Amm., pl. ii. fig. 1-3.

Amm. obliquecostatus, Ziet., Verst. Würt., p. 20, pl. xv. fig. 1.

Amm. Bonnardi, D'Orb., Terr. Jurass. Ceph., p. 196, pl. lxiv.

Ariet. Bonnardi, Wright, Lias Amm., p. 196, pl. xi. fig. 1-3.
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Ariet. Conybeari, Herbich, Széklerland, Mitth. Jahrb. ungar. geol. Anst., V. pt. 2, pl. xx. b. Ariet. multicostatus, Herbich, Széklerland, Ibid., pl. xx. a, xx. b.

Localities. — Lyme Regis, Semur, Salins, Möhringen, Vaihingen, Balingen, Waltzing in Luxemburg, Adnet.

The young of this species is smooth throughout the first volution. On the second whorl scattered folds appear, which develop into true pilæ on the third whorl.

<sup>&</sup>lt;sup>1</sup> Amm. Schwab. Jura, pl. xiii. fig. 6. <sup>2</sup> See Plate I. Fig. 17.

<sup>&</sup>lt;sup>3</sup> A similar form is figured by Quenst., Amm. Schwab. Jura, pl. vi. fig. 3, as Amm. longidomus æger.

These at first have the depressed aspect of the adult pilæ in Caloceras, and the rotundity of the abdomen increases the resemblance to this genus. On the first quarter of the fourth whorl the abdomen grows broader, flatter, and the pilæ acquire immature geniculæ. The channels make their appearance upon the second quarter of the fourth whorl, and the bent geniculæ of the adult become apparent also, though very obscure. When the lateral ridges of the sulcations are developed on the fifth whorl, the shell becomes similar to Ver. spiratissimum; and finally, as the sulcations deepen and broaden, and the geniculæ become more salient and bend more forward, the adult characteristics of the species are fully brought out.

The young as compared with the young of *spiralissimum* present considerable differences. They are broader in proportion and increase faster in bulk. Thus they form an umbilicus deeper and with fewer volutions within a given diameter than in *spiralissimum*. Five volutions of *spiralissimum* have about the same diameter as four or four and a half of *Conybeari*. There are about twenty-five pilæ on the third whorl, thirty-six on the fifth or sixth whorl, and forty on the seventh whorl.

The channels are deeper and broader, the lateral ridges and keel sharper and narrower, the sides more deeply furrowed, the pilæ more salient, and the whorl narrower from side to side in proportion to the breadth of the channel area, and narrower also in proportion to the dorso-abdominal diameter than in *spiratissimum*.

The sutures also differ considerably. The abdominal lobe in some specimens is one half deeper than the superior laterals; the inferior lateral saddles are deeper than the superior laterals, and the inferior lateral lobes shorter than the superior laterals; the auxiliary lobes and saddles continue the inclined line formed by the apices of the lobes. This anterior inclination is subject to variations in the adults of varieties. In the young the lobes and saddles are nearer to the same level, and approximate to the outlines of the sutures in *spiralissimum*. In Professor Fraas's collection there are two specimens, one in which the superior and inferior lateral lobes are about equal, and one in which the inferior laterals are a little the longer; these are both full grown.

A specimen in the Museum of Stuttgardt has a living chamber nearly one and a half volutions in length, and still incomplete.

One specimen in the Museum of Comparative Zoölogy completes nine and one half whorls without exhibiting any senile characteristics. The largest specimen yet recorded is now in the collection of the British Museum; this measured, according to Wright, about 460 mm. in diameter. The one figured by Wright, in "Lias Amm.," was 340 mm. in diameter, and old age had begun to show its effect slightly upon the last whorl. A specimen from Lyme Regis, in the collection of the Museum of Comparative Zoölogy, is associated upon the same slab with Birchii. The largest specimen in the Stuttgardt Museum was 365 mm. in diameter, and had not yet begun to exhibit very decided senile characteristics.

In the collection at Tübingen is a specimen, perhaps the same figured by Quenstedt, Plate XV. Fig. 1, with undoubted spines on the casts of the geniculæ. The original of Sowerby's figure is 455 mm. in diameter, and had begun to lose

the pilæ, but the specimen shows distinctly that the form of the adult is more compressed than in *spiratissimum*, with more convergent sides, and it has tubercules. It is precisely similar to the original of D'Orbigny's *Bonnardi* in the École des Mines. *Ver. Bonnardi* is figured by Wright as occurring in the Turneri bed, and a much more discoidal form is regarded by him as the true *Conybeari* and figured as such. The great flatness of the whorls and aspect of the whole shell in this figure are probably the effect of age. The sutures figured have senile proportions, the abdominal lobe being of about the same length as the superior laterals. The specimens figured by Hauer from the Northeastern Alps, and by Herbich from Siebenburgen, have more convergent sides and less angular geniculæ than is common in Central Europe. The variety from Luxemburg is very like the more discoidal varieties in England.

## VAR. planaries.

Amm. planaries, Fraas, MS.
Amm. Bonnardi, Oppel, not D'Orbigny.
Localitu. — Semur.

The specimen in the Museum of Comparative Zoölogy on the ninth whorl had an abdominal lobe one half longer than the superior lateral lobes, and inferior lateral saddles one half deeper than the superior laterals. The inferior lateral lobes, however, are somewhat longer than the superior laterals, and the first and second auxiliaries, which show plainly on the sides, are still longer than these. Thus the sutures appear to incline rapidly towards the umbilicus, as in Caloceras, but this is a delusion due to the peculiar proportions of the auxiliary saddles. The outlines of the superior lateral saddles are covered by the involution of the whorl, instead of being in part exposed, as in Conybeari, in which last, also, these saddles are apparently broader. The superior lateral saddles are divided by a single marginal lobe.

The pilæ begin to show senile characteristics on the first quarter of the tenth whorl, and on the second quarter of the same whorl the abdomen has suffered a diminution in breadth. Throughout the remainder of the volution there is no change in the abdomen, but the pilæ become obsolescent near its termination. The external aspect of the adult is similar to *Conybeari*.

Only one specimen of this variety occurred in Professor Fraas's collection; it is placed with Bucklandi, but its position with relation to that species was considered uncertain. Professor Fraas considers it a new species under the name of Amm. planaries, and the sutures differ greatly from those of the specimen described above, though in the form it is more like it than either of them is like Congbeari. On the last volution of this specimen the pilæ are almost obsolete, the keel more prominent, the channels considerably shallower than in the adult. The form of the whorl changes somewhat and the sides tend to converge, and the abdomen is narrower, but these changes are very slight, and due entirely to the obsolescence of the pilæ.

This form was at first identified with Bonnardi, D'Orb., but the examination of

the original at the École des Mines showed the young of the true *Bonnardi* to be tuberculated, which is not the case with the young of *planaries*. This fact was apparently not observed by Oppel, who considered *planaries* to be identical with the typical *Bonnardi*. It is possible that *Conybeari*, as figured by Hauer, may belong to this variety.

## Vermiceras ophioides, HYATT.

Plate I. Fig. 21-23. Summ. Pl. XI. Fig. 25.

Discoceras ophioides, HYATT, Bull. Mus. Comp. Zoöl., I., No. 5, p. 76. Amm. ophioides, D'Orb., Terr. Jurassique, p. 241, pl. lxiv.

Locality. - Semur.

The young is smooth for one volution and a half. On the third quarter of the second, scattered folds begin, developing into true pilæ on the first quarter of the third whorl. During the first half of this whorl, after the keel is developed, the rounded sides of the shell show that the form of the whorl, as well as the immature pilæ, resemble *Cal. laqueum*.

The abdominal sulcations are well defined on the last quarter of the third whorl, and from their well marked character on the early part of this quarter it may be inferred that they begin on the third quarter, where, however, they were not directly observed. For the same reasons, also, I should infer that there are well defined lateral ridges to the sulcations almost immediately after their first appearance on this same third quarter. The very rapid appearance of these characteristics probably prevents a repetition, or only permits a very partial one, of the adult characteristics of any of the species intermediate between Caloceras Johnstoni and Ver. Conybeari. In the course of the growth through the second quarter, the sides of the whorls remain rounded and the pilæ more or less immature, as in the adults of laqueum and Johnstoni. On the third quarter of this whorl, and simultaneously with the channels, the peculiar geniculæ and squared or quadragonal whorl appear, and we find also distinct lateral ridges to the channels, a well defined keel, and what seem to be minute tubercles, but are really only very angular geniculæ.

From this period these characteristics, which render a fragment of the adult whorl identical in its aspect with the adult of *Conybeari*, are increased and strengthened, but not otherwise changed by growth.

The sutures, however, though observed in only one specimen, differ somewhat. The lobes and saddles are more pointed and have smoother outlines than in *Ver. Conybeari*. It is a species which illustrates admirably the law of acceleration in heredity.

Canavari, in his work on the Lias of Spezia, figures under the name of *Ver.* (*Ariet.*) spiratissimum, Plate XX. Fig. 2, a very interesting dwarf, with exceedingly narrow channels and linear sunken keel. This is probably distinct, and the name supraspiratas subsequently given by this author, in his republication of this paper in the third volume of the "Memorie della Carta Geologica d' Italia," to the same

species does not appear to indicate the exact affinities. Ver. (Ariet.) Conybeari, Plate XX. Fig. 6, Ver. (Ariet.) doricus, Figs. 8-10, and abjectus, Fig. 11, all seem to be the young of some species of Vermiceras, in which keel and pilæ are developed early, possibly some form of Conybeari.

#### LEVIS STOCK.

The living chambers may be cylindrical, or they may be broadened out and considerably modified by the growth of the whorl, but the length is invariably under one volution, and often does not exceed one half of a volution. There seems to be no necessary correlation between the shape of the chamber and its length; the most attenuated and cylindrical whorls have not invariably the longest living chambers, nor the broadest whorls invariably the shortest living chambers. It is however true, in a very general way, that the longest living chambers, as a rule, occur in the Plicatus Stock among the species which have the most attenuated or cylindrical whorls.

None of the shells of the Levis Stock are directly or indirectly traceable to any known form of *Psil. planorbe*, var. *plicatum*. Their gradations and radical forms, nevertheless, do indicate derivation from *planorbe*, var. *leve*, and we must therefore consider the keels, channels, pilæ, and sutures which are similar in the two stocks as having originated independently in each stock, or, in other words, as homoplastic, and not homogenous characters.

The higher species of each series tend to become involute, and to elongate the abdomino-dorsal diameter of the whorl.

The sutures are almost purely arietian in proportions and outlines, the auxiliaries are rarely or never inclined posteriorly, the marginal digitations are less complicated, and the saddles broader and less dendritic than in the Plicatus Stock.

## FOURTH, OR CORONICERAN BRANCH.

The shells are discoidal, and involution is limited to the area of the abdomen. During senile degeneration the shell is apt to acquire flattened smooth sides and a narrow abdomen, but never loses the keel, nor becomes rounded on the abdomen, nor decreases in the amount of involution. Flattened sides and narrow abdomens may also appear in the adults of species with accelerated development of progressive characters.

#### ARNIOCERAS.

The members of this genus may be recognized by the smoothness and thin, discoidal psiloceran form of the first three or four whorls. The keel appears as an angular ridge, which develops later into a true keel. There are lateral folds in the young, which develop later into pilæ. The true pilæ appear after the keel, and then in some specimens well defined channels arise.

The form in adults is discoidal, but the whorl is quadragonal. The adult shell is discoidal; no involute forms have been found. The pilæ are prominent, thin, sharp, straight, and smooth; the geniculæ very abrupt, and on a level with the abdomen.

The sutures have immature margins, but an arietian aspect. The siphonal saddles are large and pointed; the abdominal lobe may be either equal to or much shorter than the superior lateral lobes. The latter are remarkably large and long, and the inferior lateral lobes short. This gives an elevated aspect to this portion of the suture. The superior lateral saddles are more distinctly bifid in this genus than in any other, owing to the absence, as a usual thing, of the accompanying marginal lobes of large size. The sutural margins are generally smooth or simply serrated, instead of more or less foliaceous.

The living chambers may be from one half to one volution in length.

Aged specimens are very rare, though the species are well represented by individuals. Indications of the approach of senility have been seen in some specimens, and the geratologous metamorphoses were probably similar to those of Vermiceras. Such a giant, however, as *Amm. Arnouldi*, Dum., figured in the "Études Pal. Bassin du Rhone," Plate VI., which was 274 mm. in diameter, is not described or figured as affected by senile metamorphoses, and the huge *Amm. geometricus*, Dum., Plate XXX., which was 162 mm. in diameter, had a similar history.<sup>2</sup>

#### FIRST SUBSERIES.

## Arnioceras miserabile, HYATT.

Plate II. Fig. 4-7. Summ. Pl. XII. Fig. 2.

# VAR. acutidorsale. Plate II. Fig. 4-6.

Psil. acutidorsale, Hyatt, Bull. Mus. Comp. Zoöl., I., No. 5, p. 73.

Amm. miserabile, Quenst., Amm. Schwab. Jura, pl. xiii. fig. 27-30.

Ariet. nodotianus, Wright, Lias Amm., pl. xxxvii. fig. 4, p. 300.

Amm. Macdonelli, Portl., Geol. Rep. Londonderry, p. 134, pl. xxix. A, fig. 12.

Locality. - Semur.

The lobes and saddles of one specimen in the Museum collection from Semur are shallow and broad; the inferior lateral saddles, however, taper to a blunt point. The superior lateral saddles are divided by marginal lobes more deeply than the inferior laterals, which are only serrated. The auxiliary lobes are smooth, the superior laterals deeply serrated.

The shell is smooth for the first four and three quarters volutions. Very obscure folds then begin to appear near the umbilical shoulders, and on the second quarter of the fifth whorl reach half-way across the side. These still remain, however, more prominent near the umbilicus, and are less prominent near the abdomen, which, with the exception of the keel, is perfectly smooth.

<sup>&</sup>lt;sup>1</sup> The American species Arn. Nevadanum has tubercles, but it is not yet unquestionably settled that this is an arnioceran form.

See Arn. Macdonelli, page 164.

In other young specimens, the acuteness of the abdomen begins upon the latter part of the third or first part of the fourth whorl, and the striæ of growth are regular and well marked. Previous to this the abdomen is rounded, as in *Psil. planorbe*.

The smoothness of the sides of the whorls, the immature folds, and the flat discoidal aspect of the young, make the shell very like planorbe, var. leve, and in the next stage the folds give an aspect somewhat similar to the plicatus variety of planorbe. The prolonged smooth stage of the young, before it takes on the folds, has no correspondence with any form of Caloceras, and indicates direct derivation from planorbe, var. leve. In the typical specimens of Arn. miserabile, var. acutidorsale, the folds are sometimes not apparent upon the cast, even upon the fifth whorl, but in one specimen a careful examination showed that the original shell must have had faintly marked folds, which stretched entirely across the side and had the usual abrupt terminations. Quenstedt figures this variety. The aperture is shown in his Fig. 27 to have been similar to that of planorbe, having a well marked rostrum, broad lateral sinuses, and a constriction. It is by no means certain, as Quenstedt states in the same work on page 104, that Wright's figure of the young of semicostatum, Plate I. Fig. 7 of his "Lias Ammonites," is a specimen of this species; it is quite as likely that Wright was correct. Professor Quenstedt's specimens at Tübingen are for the most part young from the Oelschiefer, but a large one 2 was nearly, if not quite, full grown. The keel in this appeared as a sharp ridge at an early age, and maintained the same character in adults.

The abdomen does not broaden out as in adult of acutidorsale, but persists in maintaining its angular character throughout life. The pilæ began quite early, but never appeared to get beyond the fold-like stage. Sometimes, however, they bend forwards and may cross the abdomen, and then the abdominal ridge forming the keel is crenulated. The variety occurs in South Germany, especially in the Oelschiefer of Quenstedt.

A form doubtfully referred to this variety was collected by Professor Orton at Ipishguanüna in Northern Peru.<sup>4</sup>

#### VAR. cuneiforme.

## Plate II. Fig. 7.

Arnioceras cuneiforme, HYATT, Bull. Mus. Comp. Zool., I., No. 5, p. 73.

Abdomen acute, as in variety acutidorsale; sides regularly convex; pilæ depressed, most prominent in the centre, and sloping gradually to either side.

The abdominal lobe is somewhat longer than the two lateral lobes, which are of about equal length. Superior lateral lobes and saddles are pointed, the inferior lateral lobes and saddles mere serrations.

<sup>&</sup>lt;sup>1</sup> Amm. Schwab. Jura, pl. xiii. fig. 27-30. <sup>2</sup> No. 7742 of his collection, locality unknown.

<sup>&</sup>lt;sup>2</sup> This does not indicate any affinity with other genera; it is a sporadic and purely pathological modification, as it is also in the young of Oxyn. Oxynotum, and many other forms in which the young shells are often affected by similar abdominal crenulations.

<sup>4</sup> Proc. Bost. Soc. Nat. Hist., XVII., 1875, p. 367.

The superior lateral lobes are slightly serrated, and the superior lateral saddles have the generic division; but otherwise the lobes and saddles are apt to be entire. These characteristics were observed in one specimen on the fifth whorl.

The general aspect of the shell is like that of the young of *Psil. planorbe*; the pilæ, however, are not merely broad prominent folds as in that species, but distinct immature pilæ, similar to those of other species of Arnioceras, and the form is quite distinct, besides being obscurely keeled. Some shells have straight pilæ and gibbous whorls, and others have bent pilæ and flatter whorls.

## Arnioceras Macdonelli, HYATT.

Amm. Macdonelli, Portlock, Geol. Rep. Londonderry, p. 134, pl. xxix. A, fig. 12. Ariet. Macdonelli, Tate and Blake, Yorkshire Lias, p. 290, pl. v. fig. 8 a-b. Ariet. nodotianus, Wright, Lias Amm., p. 300, pl. xxxvii. fig. 4.

Wright's reproduction of Portlock's figure and Portlock's own figures show that this is a most remarkable modification of *miserabile*, occurring in the Raricostatus bed, or what he first called the base of the Jamesoni bed. It is evidently an aged specimen, a very rare occurrence in this genus, and is consequently smooth. The young, however, have pilæ, and these and the section given by Portlock, the absence of channels, and compressed whorls, show it to be closely allied to *miserabile*, var. *acutidorsale*.

## Arnioceras obtusiforme, HYATT.

Plate II. Fig. 8-9 a. Summ. Pl, XII. Fig. 3.

Amm. obliquecostatus, Brauns, Der Untere Jura, pl. i. fig. 3-5.

Asteroceras obtusum (pars), Hyatt, Bull. Mus. Comp. Zool., I., No. 5, p. 79.

Locality. — Semur.

This species has the pile so closely resembling the curved depressed pile of Ast. obtusum, that it was formerly referred to that species. The young, however, are precisely similar to the young of Arnioceras, much too flat laterally for obtusum, and the pile never begin with tubercles or heavy folds, as in that species. The keel is depressed, and the channels are very shallow or absent.

#### VAR. A.

The pilæ are developed abruptly on the last quarter of the third whorl. The curved pilæ resemble those of the typical form of miserabile, var. cuneiforme.

## VAR. B.

The pilæ are developed gradually, beginning with minute, regular folds on the first quarter of the third whorl, and they continue in the adult to resemble those of *miserabile*, var. *cunciforme*, although the geniculæ become more prominent and make a nearer approach to those of *Arn. semicostatum*. The abdomen is narrow, the keel well defined, and in two specimens channels were faintly shown. The whorls of varieties A and B are both more compressed than in variety C.

#### VAR. C.

The whorls are stouter than in variety B, and acquire on the first quarter of the fourth whorl, or later, a close resemblance to those of *semicostatum*. The inferior lateral saddles are considerably deeper than the superior laterals, the inferior lateral lobes considerably shorter than the superior laterals, and pointed. The sutures were observed upon the latter part of the fifth whorl.

#### SECOND SUBSERIES.

#### Arnioceras semicostatum, HYATT.

Plate II. Fig. 10-16. Summ. Pl. XII. Fig. 4.

Amm. semicostatus, SIMPSON, Amm. of Yorkshire Lias, p. 51.1

Ariet. semicostatus, WRIGHT, Lias Amm., pl. i. fig. 7 (not fig. 4, 5, 8).

Arn. semicostatum, HYATT, Bull. Mus. Comp. Zoöl., I., No. 5, p. 74.

Localities. - Whitby, Semur, Basle, Spezia.

#### VAR. A.

## Plate II. Fig. 10, 16.

During the first four and three quarters or five volutions, the shell closely resembles Arn. miserabile, var. acutidorsale. After this the pilæ appear. They are at first broad and depressed, but possess the sharp definition of true pilæ, and terminate abruptly on the edge of the abdomen. The abdomen is rounded, and the keel a distinct though depressed ridge. Its time of appearance could not be determined, but it was plainly apparent on the second or third quarter of the fifth whorl, and previous to this the aspect of the abdomen was precisely that of miserabile, var. acutidorsale.

## VAR. B.

#### Plate II. Fig. 11-14.

In this variety the young resemble very closely the adults of Arn. miserabile, var. acutidorsale. The pilæ make their appearance earlier than in variety A, but, while becoming more numerous, often retain their fold-like aspect, and terminate abruptly near the abdomen. The keel appears about the same time as the pilæ, and may be either with or without slight channels. In some specimens the whorls become stouter than usual in the adult, and the geniculæ prominent. In one specimen they are inclined posteriorly.

In the Museum of Stuttgardt there are three specimens of this variety, one from Behla and one from Muhlfingen (No. 4688), both in the Geometricus or Upper Bucklandi bed. Another from Filder was found in the Angulatus bed.

¹ This name does not appear in the first edition of Morris's Catalogue, 1843, but is found in the second edition, 1854, as Amm. semicostatum, Y. & B., Geol. Yorkshire, p. 257. This is an erroneous reference, since no such species was described in that work. In the Museum of Yorkshire is a specimen with this name, and it was described by Simpson in his Monograph of the Ammonites of the Yorkshire Lias, which was not cited in Mr. Morris's first edition, though published in 1843.

#### VAR. C.

The adults are remarkable for their prominent straight keels. The channels when present are very shallow. The young remain smooth for a longer time than in other varieties. The pilæ appear between the first quarter of the fourth and first quarter of the fifth whorl.

While smooth throughout the first three or four whorls, it is identical with the adults of *miserabile*, var. *acutidorsale*, but the sutures are more immature. The pilæ develop quickly, and are similar to those of variety B. In fact, the young can be distinguished only by the larger size, quicker growth, and smaller number of the pilæ. Associated with these are specimens with compressed whorls, perhaps males.

#### VAR. D.

## Plate II. Fig. 15, 15 a.

This has a narrow abdomen, and the pilæ are more prominent near the dorsum. They appear on the fourth quarter of the third, or on the first half of the fourth whorl, earlier than in some specimens of variety B, and are more slowly developed. Some of the young are very like the adult of *Arn. miserabile*, var. cuneiforme. The pilæ bend forward when they first appear, or soon after, as in this variety, although subsequently becoming straight, like those of the adults of variety A. The abdomen is sharp, as in miserabile, var. acutidorsale; the keel does not appear until the pilæ begin to acquire their prominent, straight adult characteristics. The sutures have serrated outlines.

The abdominal lobe (Plate II. Fig. 15 a) may be equal to the superior lateral lobes, or one fourth shorter, and the siphonal saddle is remarkably large. The superior lateral saddles are divided symmetrically, and are equal in depth to the inferior laterals. The superior lateral lobes are very broad, and about one half longer than the inferior laterals. These characteristics were observed on the third quarter of the fifth volution of a specimen from Semur. In specimens from Whitby, on the second quarter of the same volution the sutures are similar in all respects, but the superior lateral lobes are at first equal to the abdominal lobe in successive sutures, and then slightly longer. At still earlier stages, when the marginal lobes first appear, the abdominal lobe is usually of the same depth as the superior laterals, or shallower (Plate II. Fig. 15 a). One specimen from Semur had sutures maintaining these immature proportions even on the latter part of the fifth whorl.

There are several specimens from Spezia in Bronn's collection, Museum of Comparative Zoölogy, labelled by Capelini Anm. subarictinus, Menegh. These seem to belong to this species, but are so compressed that it is difficult to make sure of the identification. The young are smooth until a very late stage, as is usual in semicostatum, and the pilæ and form are also similar. They are in the yellow clayey shale, and described as from Coregna near Spezia.

#### Arnioceras Hartmanni, HYATT.

Plate II. Fig. 17, 18. Plate III. Fig. 1, 1 a. Summ. Pl. XII. Fig. 5.

Amm. Hartmanni, Oppel, Der Jura, p. 79; Würt. Jahresh., XII. p. 199.
Amm. geometricus, Oppel (pars), Ibid.
Arn. kridiforme, HYATT, Bull. Mus. Comp. Zoöl., I., No. 5, p. 74.
Amm. kridion, D'Orb., Terr. Jurass. Ceph., p. 205, pl. li.
Amm. falcaries (pars), Quenst., Amm. Schwab. Jura, pl. xiii. fig. 21.
Amm. robustus (pars), Quenst., Ibid., fig. 22.

Localities. — Whitby, Lyme Regis, Semur, Bonnert, Suabia, Gmünd, Adnet.

This species has more compressed adult whorls than any variety of *Arn. semi-costatum*, and, although the pilæ are similar, they begin to appear at an earlier age and are developed more gradually. The abdomen is also in many specimens, though not in all, distinctly channelled, and the keel prominent.

In one specimen the superior lateral lobes are nearly as long as the abdominal lobe on the sixth whorl, and on the same whorl in another they were two fifths shorter. The inferior lateral saddles are deeper than the superior laterals, and the inferior lateral lobes very short.

A specimen in the Museum of Stuttgardt, collected by Prof. Fraas, is from Arietenkalk, Hechingen (No. 5026 of that collection); another, from Gmünd, was found in the Geometricus bed, and is labelled *Amm. Nodotianus*, D'Orb. Two others, from Behla, are labelled *Amm. falcaries*, Quenst.; these belong to his sparsely ribbed variety, which is just intermediate between *Arn. Hartmanni*, and some varieties of *Arn. semicostatum*.

A specimen of falcaries, Quenstedt, figured by him, is described as partly unrolled. Examination of the broken end, however, shows that a calcareous worm tube has occasioned the distortion by having been built upon the abdomen of the growing shell. This is a common occurrence, and was observed in several specimens at Semur. There are others, however, in which this distortion, as in other species of Ammonitinæ, takes place without the presence of any foreign body between the whorls. Such examples have been named Crioceras Eryon and Mandubuis by Reynés. These and other cases show the kind of error likely to occur from the use of such names as Crioceras, Gyroceras, etc.

The flattened sides and general aspect of Quenstedt's figure of falcaries robustus <sup>2</sup> agrees apparently more nearly with this species than any other known to me. This species is the one commonly named Amm. geometricus, Oppel, in the collections in Germany, and seems to have been in part confused with that species by Oppel.

<sup>&</sup>lt;sup>1</sup> Der Jura, pl. viii. fig. 6.

<sup>&</sup>lt;sup>2</sup> Amm, Schwab, Jura,

## Arnioceras tardecrescens, HYATT.

Plate II. Fig. 19, 21-22. Summ. Pl. XII. Fig. 6.

Amm. tardecrescens, Hyatt, Bull. Mus. Comp. Zoöl., I., No. 5, p. 74.
Amm. tardecrescens, Hauer, Ceph. Lias Nordöstl. Alpen, p. 20, pl. iii.
Amm. falcaries (pars), Quenst., Der Jura, pl. vii. fig. 7 (not fig. 6).
Amm. fulcaries densicosta, Quenst., Amm. Schwab, Jura, pl. xiii. fig. 7.

Localities. - Yorkshire, Semur, Durrenburg.

The pilæ appear on the fourth whorl at variable times. There are fewer whorls, and they are wider from the abdomen to the dorsum and have generally rounder sides, than in Arn. Hartmanni.

The abdominal lobe is equal to or somewhat longer than the superior laterals; the inferior lateral saddles are shallower than the superior laterals, and the inferior lateral lobes are much shorter, sometimes a third less, than the superior laterals on the last quarter of the sixth volution. On the third quarter of the same whorl in the same specimen from Semur, the abdominal lobe was one half shorter than the superior laterals. The siphonal saddle was very large, and the superior lateral lobes very long and broad, with straight sides, the inferior lateral lobes two fifths shorter than the superior laterals. The first auxiliary saddles are visible on the sides. The marginal lobes are still hardly more than mere serrations, except along the bases of the saddles. The superior lateral lobes have very broad and minutely serrated summits.

A specimen in the Museum of Stuttgardt had curious characteristics. The sutures are undoubtedly arnioceran, the keel very prominent, and the channels shallow. The form of the whorls and the pilæ, however, are similar to those of Conybeari. Another specimen from Boihingen is precisely similar, but the pilæ terminate abruptly at the geniculæ somewhat below the edges of the channels, instead of being continued upwards and forwards, as in the former and in Conybeari. Neither of these shows the young whorls well enough to enable one to identify them accurately either with Arn. Hartmanni or Arn. tardecrescens, but they are undoubtedly arnioceran forms. Both are referred to the Geometricus zone.

The original of Quenstedt's figure in Der Jura, from Pforen, Baden, named Amm. falcaries, has the narrow sulcated keeled abdomen, rounded sides, and pilæ of this species. There is also from Achdorf in Baden a specimen about 26 mm. in diameter, which just begins to show the pilæ. The figure by Quenstedt<sup>2</sup> shows a form in which the young is smooth for a considerable number of whorls.

 $<sup>^{1}</sup>$  This may be the specimen figured in Amm. Schwab. Jura, pl. xiii. fig. 18, as Amm. falcaries levissimus.

<sup>&</sup>lt;sup>2</sup> Amm. Schwab. Jura, pl. xiii. fig. 7.

# Arnioceras ceras, L. Agassiz. Plate II. Fig. 20, 20 a.

Arnioceras ceras, L. Agassiz, Bull. Mus. Comp. Zoöl., I., No. 5, p. 74.

Amm. ceratitoides, Quenst., Amm. Schwab. Jura, pl. xiii. fig. 10 (not fig. 8, 9, 11).

Amm. Turneri, Quenst., Ibid., pl. xix. fig. 6-8 (not fig. 5-9).

Amm. ceras, Hauer, Ceph. Lias Nordöstl. Alpen, p. 25, pl. vi. fig. 4-6.

Localities. - Semur, Whitby, Lyme Regis.

This species approximates to the aspect of Coroniceras, and also imitates closely the general form and characteristics of some varieties of Ast. Turneri. Both in England and Germany, when the interior of the umbilicus or the smooth compressed younger whorls are not preserved, even the most acute observers are apt to consider the adult whorl as belonging to Turneri. Some of Quenstedt's figures, especially Fig. 8, Plate XIII., may be either ceras or some allied species of Arnioceras. The keel is prominent, the channels are broader and deeper than usual, the geniculæ are prominent and slightly bent forward, the sides, however, flat and slightly convergent, and the pilæ straight and smooth, as usual in this genus. The pilæ begin upon the third quarter of the fourth whorl.

The superior lateral lobes are somewhat longer than the abdominal lobe. The inferior lateral saddles are one fourth deeper than the superior laterals, the inferior lateral lobes one half shorter than the superior laterals on the latter half of the sixth volution.

A specimen in the Museum of Stuttgardt, locality uncertain, is referred to the Geometricus zone. Two young specimens from the Bucklandi zone, labelled Bucklandi (No. 2756), in Quenstedt's collection, also probably belong to this species. The young are smooth, and the form differs from that of typical ceras only in being a trifle stouter. The channels, perhaps, also appear at quite an early period, but this sometimes occurs in specimens of the typical form. There is also a large specimen from Jettenburg.

What appeared to be very close allies of this species were collected by Professor Orton at Ipishguanüna, in Northern  $Peru.^1$ 

# Arnioceras Bodleyi, HYATT.

Plate II. Fig. 23-24 a. Summ. Pl. XII. Fig. 7.

Amm. Bodleyi, BRUCK., Murch. Geol. Cheltenh., pl. ii. fig. 7.

Amm. ceratitoides, Quenst., Die Ceph., pl. xix. fig. 13; Amm. Schwab. Jura, pl. xiii. fig. 8, 9, 11.

Amm. geometricus, Oppel (pars), Der Jura, Würt. Jahreshf., XII. p. 199.

Ariet. semicostatum, WRIGHT, Lias Amm., pl. i. fig. 4, 5, 8 (not fig. 7).

Arn. falcaries, HYATT, Bull. Mus. Comp. Zool., I., No. 5, p. 74.

Ariet. difformis, Blake, Yorkshire Lias, p. 289, pl. vi. fig. 3 a, b.

Localities. - Whitby, Bonnert, Semur, Raidwangen, Basle, Salins.

There are three varieties in this species; one, variety A, figured on Plate II. Fig. 23, has stout, thick whorls; the second, variety B, has flattened whorls; and the third, variety C, figured on Plate II. Fig. 24, has flattened whorls like those of the second variety, but they are somewhat wider on the sides.

Proc. Bost. Soc. Nat. Hist., 1875, XVII. p. 366.

Varieties B and C, from Semur, showed tubercular-like folds on the latter part of the first, and part of the second whorl, which were continued on the umbilical border of the succeeding whorls, gradually developing into true pilæ on the third whorl.

For a short interval in the specimen of variety A the shell is smooth again, and in that of variety C the folds still remain apparent, but so depressed that they were made out with difficulty. On the first quarter of the third whorl in one specimen of variety B, and the third quarter of a specimen of variety C, the folds reappear on the umbilical border, but develop so gradually that lateral pilæ are not produced until the latter part of the first quarter of the fourth whorl. Several other specimens of these same varieties, however, from the same locality, did not show the psiloceran folds in the young, or differ from those of variety A.

A fragment from Ramert in the Museum of Stuttgardt is the true *ceratitoides* of Quenstedt, which differs from *ceras* in having a more prominent, narrower abdomen and shallower channels.

A specimen of the stout variety from Cheltenham, named *Bodleyi*, Bruck., has well preserved young which show this species to be closely allied to *ceras*. The thinner variety described above has the young much compressed, and similar to the adult of the Cheltenham specimen. On the other hand, the young of the Cheltenham specimen is precisely like the adult of *Arn. Hartmanni*. Oppel's description shows that he identified the compressed variety as the *Bodleyi* of Bruck., and the stout varieties as *Amm. geometricus*.

## Arnioceras falcaries, HYATT.

Plate II. Fig. 25-27.

Amm. falcaries, QUENST., Der Jura, p. 70, pl. vii. fig. 6 (not fig. 7).

Amm. falcaries, QUENST., Amm. Schwab. Jura, pl. xiii. fig. 12-14.

Arnioceras incipiens, HYATT, Bull. Mus. Comp. Zool. I., No. 5, p. 74.

Amm. acuticarinatus, SIMPS., Museum at Whitby?¹

Amm. Youngi, SIMPS., Mon. Amm, p. 46?

Localities. — Semur, Robin Hood's Bay, Balingen.

The sides are convex, the whorls compressed, and the abdomen obtusely angular, keel prominent. The pilæ begin with a line of tubercles, which appear on the first half of the fourth whorl, preceding the true pilæ by about one fourth of a whorl. The pilæ are not strongly developed upon the umbilical shoulders of the whorls, which in many specimens are almost smooth.

Variety A, figured on Plate II. Fig. 25, 26, has prominent geniculæ and keel without channels, but some specimens leading to the next variety have less prominent geniculæ.

Variety B has less prominent pilæ and keel. The channels, though mere linear depressions, begin to appear in some specimens.

Variety C, figured on Plate II. Fig. 27, has even less prominent pilæ, but a keel with distinct narrow channels, and in some specimens the pilæ were developed abruptly, not being preceded by the usual line of tubercles.

 $^{1}$  The ? in these cases is due to the fact that I was not permitted to examine the originals in the Museum at Whitby.

The shell of variety A is smooth for three or three and a half volutions; the tubercles begin to spread entirely across the sides on the first quarter of the fifth whorl, and about this time the geniculæ have become prominent. The channels are not present in any of these specimens, but more or less faintly marked narrow depressed zones may be observed on either side of the keel. This variety leads directly into the next, in which the depressed zones become channels. The geniculæ differ in aspect from those of variety A, because they abut against the well defined lateral ridges of the channels.

Variety B has the pilæ developed at about the same period as in variety A, but the channels appear in the young, and on the second quarter of the fifth volution they are quite distinct.

There is one specimen of variety A in which the pilæ are slightly inclined posteriorly, and the geniculæ more prominent than in any other specimen. A very slight sinking of the abdomen in this specimen would produce a form of variety C, which is found at Robin Hood's Bay in England, and which has a keeled, channelled, and flattened abdomen. The single suture which was exposed in this specimen possessed remarkably pointed and serrated superior and inferior lateral saddles, and very broad, rounded, but serrated superior lateral lobes. The auxiliary saddles and lobes were pointed and serrated. There was a very large siphonal saddle, and all of the larger lobes and saddles appeared of about the same depth and length.

One specimen of this species from Balingen was received in exchange from the Museum of Stuttgardt, under the name of Nodotianus. Two specimens in Quenstedt's collection belonged undoubtedly to this species, variety A. One from Lias, a, Pforen, named Amm. falcaries (No. 4428), and one from Göppingen (No. 11182), were in the Arietenkalk. The last was 63 mm. in diameter and a typical form of variety A; the pilæ are, however, inclined posteriorly, while in the other they are pointed forwards. In the specimen from Pforen the pilæ begin abruptly near the abdominal side unpreceded by tubercles. Other specimens, especially the original of his figure, Plate VII. Fig. 6, also from Pforen, show that Hartmanni and this species have intermediate varieties.

Several forms are found in the Semur collection under the name of *Hettangensis*, Rey., one of which has smooth young, with fine pilations and an adult whorl having close resemblances to this species and also to *Arn. miserabile*, var. acutidorsale.

#### THIRD SUBSERIES.

#### Arnioceras kridioides, HYATT.

Plate II. Fig. 28, Summ. Pl. XII. Fig. 8.

Ophioceras kridioides, Hyatt, Bull. Mus. Comp. Zool., I., No. 5, p. 75.

Amm. kridion, Quenst., Der Jura, pl. vii. fig. 8, Amm. Schwab. Jura, pl. xi. fig. 5, 6 (not fig. 7).

Amm. Bucklandi carinaries, Quenst., Amm. Schwab. Jura, pl. xi. fig. 3.

Localities. — Basle, Semur.

This species approximates in aspect to Cal. raricostatum, and was on this account at first erroneously referred to that species. The shell is, however,

smooth, as in Arnioceras, on the first three whorls, the pilæ being acquired only on the last quarter of the third or first quarter of the fourth volution. They are only about twenty-five in number on the fourth whorl, and gradually decrease in number on subsequent whorls.

The sutures on the second quarter of the sixth whorl show close affinity for Arn. semicostatum. This resemblance ceases in a great measure after the beginning of the fifth volution, when the pilæ assume an aspect similar to those of Cal. raricostatum. The resemblance is due to the fact that the pilæ remain undeveloped; if they become more prominent, the shell would be more like semicostatum. The keel is also not so well developed as in semicostatum, and on this account resembles that of a species of Caloceras. The abdominal lobe at this time is slightly longer than the superior laterals, and these are about one half longer than the inferior laterals. The superior lateral saddles are broad, shallow, and deeply divided by only one marginal lobe. The inferior lateral saddles are tongueshaped, and slightly deeper than the superior laterals. The lobes and saddles are serrated, and the first auxiliary saddle is very small. There are four specimens in the Museum of Stuttgardt which entirely confirm these observations. They are from Behla, and labelled Amm. kridion, Quenst. One is more compressed than the other, and closely approximates to Arn. semicostatum; in fact, the young shell is quite as smooth as the gibbous variety of that species, and with the exception of the abdomen, keel, and sutures it is identical with it.

The original of Quenstedt's description from Bebenhausen, the type in Suabia, bears out these remarks in every particular; but in his "Ammoniten des Schwäbischen Jura," Figure 7 has channels and a form not identical with others of this species, all of which are similar to the young of *Cor. kridion* during the adult stage.

## Arnioceras? Nevadanum, HYATT.

Amm. Nevadanus, Gabb, Am. Journ. Conch. Philad, V., 1869, p. 6, pl. iii. fig. 1; IV. pl. xvi.

This interesting form was found near Volcano, in Nevada, and probably belongs to the Lower Lias. The young as figured by Gabb is smooth, and the late stage at which the pilæ were introduced, their linear, straight aspect, and crowded arrangement throughout the young whorls, are unquestionably arnioceran. The sutures also, as figured in Volume IV. Plate XVI., have the characteristic outlines of this genus. Nevertheless, the older whorls have the form and proportions of *Ver. Conybeari*, and are also tuberculated, the abdomen being keeled and channelled. The abdomen has, however, much broader channels than any specimens of Vermiceras yet observed. The character of this part is evidently not unlike that of the specimen in the Stuttgardt Museum described in note to page 70 as occurring in the Angulatus bed and yet having channels

<sup>&</sup>lt;sup>1</sup> The species associated with this by Gabb, under the name of *Amm. Colfaxi* (Am. Journ. Conch., 1869, V. p. 7, pl. iv. fig. 2, IV. pl. xvi.), and reported as found in the Lias on the western slope of the Sierra Nevada near Colfax, was in poor condition, and was consequently so badly represented in the figure as to be indeterminable.

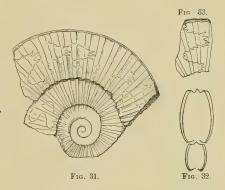
with entire lateral ridges, which occupy nearly the whole breadth of the abdomen. Gabb's figures are a little at variance with his description on this point, and may have been taken from different whorls; one in Volume V. has narrow channels, while the section in Volume IV. Plate XVI. has broad channels. The section, description, and sutures show lateral distortion. If it were not for this and the possible errors of the figures, we should be positive that it was a tuberculated arnioceran form.

## Arnioceras Humboldti, HYATT.

Locality. - Humboldt County, Nevada

This species is closely allied to *Arn. tardecrescens*, from which, however, it differs in the sutures and proportions of the whorls, those of the latter being broader in proportion to their breadth. This species also probably reached a larger average

size and had a thicker shell. It differs from Arn. Bodleyi in the same characters, and the sides are less divergent outwardly than in that species, and not so flat. The great thickness of the shell reminds one of Arn. Hartmanni, but the whorls increase faster by growth in the abdomino-dorsal diameter, and it has a smaller number of whorls at the same age. The figures are close to the natural size, and give accurately the proportions of the fossil. The actual diameter of the fragment represented in Figure 31 is 48.5



mm., and the keel is a trifle more prominent than it appears in the drawing. The pilæ were much abraded and are truthfully portrayed in this figure, but when entire they possessed the usual sharpness of the genus Arnioceras.

The transverse section represented in Figure 32 is in part a restoration, and has been slightly reduced in the cut. The extreme breadth of the side and keel is 19.5 mm. The sutures are given with sufficient accuracy in Fig. 33, but the median lobe which divides the superior lateral saddles has been overlooked, and the abdominal lobe has not been indicated. The latter has the usual arnioceran proportions, being somewhat shorter than the superior laterals. The marginal lobe dividing the superior lateral saddles is unusually broad, and in fact the broad massive aspect of the two lateral saddles is a marked characteristic of these sutures.

In the collection of the Mining Bureau at San Francisco is a specimen of Arnioceras, which, judging from a hasty sketch, resembles this species. It was labelled as coming from Inyo County, California, but we were not able to verify the locality. It is, however, quite certain that species of the Lower Lias have been found in the West in the regions occupied by the exposures of the Jura.

Geyer, in his "Ceph. Hierlatz b. Hallstadt," gives figures and descriptions of the following species of this genus. Arn. (Psil.) abnorme and Suessi; Arn. (Ariet.) semilevis, Plate III. Fig. 7, a channelled form like Arn. ceras; Arn. (Ariet.) ambiguus, and (Ariet.) of Quenstedt, Plate III. Fig. 14; the last is probably the same as Arn. cunciforme, and probably the same as his undetermined species of Amphiceras figured on Plate II. Fig. 30. Hauer, in his "Ceph. Lias Nordöstl. Alpen," gives figures and descriptions of Arn. (Amn.) difformis, which may be the same as semilevis, Geyer, though channels and keel are both figured as preceding the pilæ in his Plate VII. Fig. 12. His young specimen, Plate VII. Fig. 9, named Amm. multicostatus, is probably also a species of Arnioceras; but the larger specimen, Plate VII. Fig. 7, 8, is a coroniceran form. All of these were from Hierlatz.

#### CORONICERAS.

The young are stouter than in Caloceras or Arnioceras, and smooth for a shorter period, and the stage following this usually has tuberculated pilæ and a whorl with more or less divergent sides. The abdomen in the adult is keeled and channelled, the sides parallel or slightly convergent, the pilæ being prominent and heavily tuberculated. In the old, the tubercles are lost, the channels obsolete, the keel very prominent, the abdomen very narrow, and the outline of the whorl in section trigonal.

The abdominal lobe in adults is deep and narrow, the superior lateral saddles are generally shallower than the inferior laterals, and the first auxiliary lobes and saddles are of comparatively small size. The great length of the abdominal lobe, the shallowness of the superior lateral saddles, the small size of the first auxiliary saddles, and the shortness and comparatively small size of their corresponding superior and inferior lateral lobes, give great prominence to the inferior lateral saddles. The outlines of the sutures are also much complicated, the marginal lobes being broader and longer than is usual in this family. In old age the abdominal lobe becomes shorter, often only slightly exceeding the superior laterals in length. Degeneration also takes place in other lobes and saddles, especially on the margins. The oldest sutures are, therefore, simpler than those of the adult.

The first subseries has heavily tuberculated pile, and the whorl is very gibbous near the umbilical shoulder.

The second subseries has the tubercular and inner portions of the pilæ more nearly equal in prominence, the whorls are not usually so stout or numerous, and the abdomen has a flatter outline.

The third subseries is apt to have young with broader abdomens than in the first two, and the pilæ are frequently divided in the nealogic stages. Massive whorls and pilæ are characteristic of the first senile stage in the larger shells.

<sup>&</sup>lt;sup>1</sup> Amm. Suessi, Hauer, Unsym. Amm. Hierlatz-Schichter, Sitz. Akad. Wien, 1854, XIII. pl. i. fig. 1-6, and the figures of Geyer, show that this species has not, as supposed by Rolle, Sitz. Akad. Wien, 1857, XXVI., and by Stur, Geol. d. Steirmark, any close affinity with Hagenowi from the Bone bed of the Waldhäuser Höhe near Tübingen.

FIRST SUBSERIES.

## Coroniceras kridion, HYATT.

Plate III. Fig. 2, 3. Summ. Pl. XII. Fig. 9.

Amm. kridion, Ziet., Verst. Würt., pl. iii. fig. 2.

Amm. kridion, Hauer, Ceph. Nordöstl. Alpen, pl. iii. fig. 4-6.

Localities. — Semur, Stuttgardt, Balingen.

The pilæ were already visible on the first part of the third whorl, but when they began could not be ascertained. On the first quarter of the third whorl the flattened abdomen of the younger volutions became more elevated, and the keel was introduced. The keel continued to increase in prominence thereafter, but the channels, which are faintly visible on the fourth whorl, only broaden out, and do not sensibly increase in depth, after they reach the last part of the fifth volution.

The form acquired on the third or fourth whorl is carried throughout life, the sides curving evenly from the dorsum to the abdomen; the abdomen is elevated, the pilæ are either overhanging or slightly tuberculated on the latter part of the third whorl, but very soon the curvature becomes equal and the tuberculations disappear, though the geniculæ sometimes remain very prominent even on casts. There are three specimens of this species in the Museum of Stuttgardt, the exact position of which, with relation to Bucklandi, is considered uncertain by Professor Fraas. The young in all these specimens are smooth, and precisely similar to the young of the specimens from the Angulatus bed, from which the adults, however, differ slightly. The tubercular processes on the casts, as in all other specimens of this species, are blunt, and covered smoothly by the shell, not protruding into spines. The specimens in the Bucklandi bed have longer, stouter whorls, with different sutures, but these differences are not sufficient to separate them; they are probably closely allied direct descendants.

Oppel claimed to have had the original of Zieten's description, and, according to him, it is a species like *Conybeari*, which is found with and under *Bucklandi*. The above is the only species answering to this description and agreeing with Zieten's figure in having tuberculated pilæ, slightly divergent sides, a raised abdomen, and prominent keel. There are no channels in Zieten's figure, but his specimen was young, and even in the full-grown *kridion* they are very shallow. Two adults and three young specimens from Möhringen, labelled *Bodleyi* (No. 3977), are in the Museum of Stuttgardt, from the Angulatus zone. The casts appear to be identical with *Annn. Caprotinus* D'Orb., but the apparent tubercles were merely covered smoothly by the shell, and not continued out into points. Besides these specimens there is a fossil from Filder (No. 3978), which is precisely like Zieten's figure, and confirms these identifications.

Though there is close approximation in the characteristics of the young in most forms, there are sometimes differences. The young of the normal forms

<sup>&</sup>lt;sup>1</sup> Zieten's original I was not able to see; it could not be found in the Museum at Munich during my visit.

often have broad and gibbous whorls, like the young of sinenuriense, and the pilæ and sutures are also sometimes quite similar to those of that species.

A specimen of this species occurs in the Scipionis bed of the collection at Semur, in company with the *Amm. Hehli* of Reynés, from some representatives of which it cannot be distinguished.

## Coroniceras coronaries, HYATT.

Amm. coronaries, Quenst., Der Jura, p. 68, pl. vii. fig. 5; Amm. Schwab. Jura, pl. xvi.

Quenstedt's original is a very large cast, 470 mm. in diameter, and has about thirteen whorls, with the young showing in the centre. It differs from variety  $\bf A$  of *rotiforme* in persistently maintaining throughout life the breadth and elevation of the abdomen, together with the keel, channels, and ridges.

The adult, though much larger, is similar to kridion in its heavy overhanging pilæ, divergent sides, and broad, elevated abdomen. The young with its large pilæ and prominent geniculæ is similar to the young of some varieties of rotiforme. There is a broad space on either side of the abdomen, which even in Quenstedt's large specimen is not covered by the succeeding whorl, a character also present, though not invariable, in the adults of rotiforme and kridion. Quenstedt's figure shows the undiminished dorso-abdominal diameter of the last whorl, and the effects of senile degeneration in the pilæ; these last, having lost the geniculæ, thus become reduced to massive bent folds. The form has been changed somewhat, but nevertheless the keel, channels, and even the lateral ridges, are persistent.

The sutures, though evidently senile, still have an abdominal lobe longer than the superior laterals, but the marginal lobes and saddles have degenerated more markedly.

## Coroniceras rotiforme, HYATT.

#### Plate III. Fig. 4-17b.

Amm. rotiforme, Sow., Min. Conch., V. p. 76, pl. ecceliii.
Amm. rotiforme, Ziet., Verst. Würt., p. 35, pl. xxvi. fig. 1.

Amm. rotiforme, D'ORB., Terr. Jurass. Ceph., p. 293, pl. lxxxix. fig. 1-3.

Amm. rotiforme, HAUER, Ceph. Nordöstl. Alpen, pl. i. fig. 1, 2; pl. ii. fig. 7-9.

Amm. rotiforme, Quenst., Amm. Schwab. Jura, pl. xv.

Ariet. rotiforme, WRIGHT, Lias Amm., p. 278, pl. v. fig. 1-4; pl. vii. fig. 1 (not pl. ix. fig. 1-3).

Localities. - Semur, Stuttgardt, Vaihingen, Balingen.

#### VAR. A.

## Plate III. Fig. 4, 10, 14-16.

This has smooth young during one or more, but rarely throughout two volutions. Large, coarse approximated tubercles then appeared, and rapidly developed into folds, which became more widely separated on the first quarter of the third whorl, and acquired the aspect of the adult pilæ of *Cor. kridion*. The keel appeared on the third quarter of the third whorl, but remained a mere ridge, until the advent of the channels about one volution later, when it became

<sup>&</sup>lt;sup>1</sup> In the adult stage the abdominal lobe was undoubtedly much longer in proportion.

more prominent. Upon either the latter part of the fourth, or first quarter of the fifth volution, the whorl attained its adult characteristics.

During the first volution the increase laterally had been very great, forming a deep umbilicus; subsequently the tubercles and folds were added to the width of the abdomen of the earlier whorls, giving a general resemblance to Cor. latum. The young whorls of specimens in which the tubercles appeared later on the third whorl were usually rounder, and exhibited, when seen from the side, only a very remote resemblance to Cor. latum. These passed suddenly, so fast did the tubercles grow to be folds and then true pilæ, into the stage in which they resembled Cor. kridion. After this stage, the preponderance of the abdominal region is not so marked, though it may be maintained throughout the fourth volution. Quenstedt's young specimen, with a living chamber one volution in length, exhibited a broad abdomen on the fourth whorl.

The geniculæ are at first not tuberculated, but sharp and angular, as in some varieties of Cor. kridion. The abdomen, however, does not usually become sufficiently prominent in the earlier stages of growth to bear comparison with that region in kridion. After this period the umbilical shoulders are developed more proportionally, and finally on the fifth volution the whorl becomes broader dorsally than near the abdomen. The dorsal curves of the pilæ become more prominent, and sink or are contracted to form the tubercular geniculæ. These, subsequently bend forward in some specimens, ascending the abdomen. This last character may occur earlier, on the third whorl, or, on the other hand, be omitted altogether, even in adults.

This description of the stages of development may be curiously altered by a malformation of the abdomen. The pilæ, Plate III. Fig. 7, 11,<sup>2</sup> are continued across, cutting up the abdomen into a series of waves entirely obliterating the keel and channels.

This variety has young which differ considerably from one another in the relative breadth of the abdomen, some being excessively broad and flat during the young whorls, and others, especially the microceran forms, have much narrower whorls. The number of the pile also differs, these parts being more widely separated in the broad, flat young than in others.

In the majority of adult specimens, the superior lateral saddles are deeply divided by two marginal lobes, and spread out laterally beyond, or on the geniculæ. One specimen, however, from Semur, though not differing in other respects, has superior lateral saddles so long and narrow that the superior lateral lobes occupy the genicular line. The abdominal lobe extends beyond the superior laterals by about one third, and the superior lateral saddles are of about the same depth as the inferior laterals, though much broader.

#### VAR. B.

This variety is founded on two specimens, which maintained a broad abdomen and the immature, thick, unshapely pilæ of the young until a late

<sup>&</sup>lt;sup>1</sup> Figured in Amm. Schwäb. Jura, pl. xv. fig. 9.

<sup>&</sup>lt;sup>2</sup> Fig. 7 represents the abdomen erroneously, the forward projections of the pilæ where they meet on the abdomen being flattened out in the specimen.

stage of growth. The lobes and saddles also remained immature, and the pile were in some instances divided. They resemble Cor. latum in the rounded outline of the superior and inferior lateral saddles, but are unquestionably rotiformian in the equal height of the saddles, and in the prolonged and slender marginal lobes.

#### VAR. C.

#### Plate III. Fig. 17.

This is not the *Amm. caprotinus* of D'Orbigny, as I supposed in my first review of this species, but a local variety of *Cor. rotiforme* found at Semur. The tubercles are very distinct and prominent, and the pilæ are thicker and more decidedly depressed as they approach the tubercles than in variety B. Wright's figure of Sowerby's original, and his other figures, show affinity with this variety; but it is not practicable to identify them with other varieties as they are here described.

During the first senile stage, on the second quarter of the tenth whorl, the keel and channels may be even more elevated than in the adult, but smooth zones appear on either side of the channel ridges. The geniculæ, whose tuberculated bends are also lower on the sides than in the adult, do not terminate, as in that stage, close to the channel ridges, but on the outer edges of the smooth intervening zones.

The abdominal lobe at this period is only one fourth longer than the superior laterals, and the inferior laterals are about one tenth shorter than these last. There is evidently a tendency, as in other cases of senility, to return to the immature proportions of the young.

In the next senile stage the pilæ began to lose their prominence and their tubercles, and on the last quarter of the tenth whorl the latter had entirely disappeared. The abdomen also became more prominent on account of these changes, and marked alteration in the outline of the whorl occurred still later in the more advanced stages of degeneration. The flattening and convergence of the sides, however, really began with the advent of the smooth zones, and this was the beginning of the metamorphoses which in later stages materially altered the outline of the whorl. The keel became more prominent on account of the greater shallowness of the channels, though these still retained their lateral ridges. A slight increase in the breadth of the sides at this stage would have produced a whorl in all respects like *Cor. orbiculatum*.

Several collections were closely examined for this purpose, but they did not contain many young specimens. We found it difficult to trace the likeness of the young *roliforme* to the adult of *kridion*, on account of the much greater gibbosity of the whorls in the ordinary forms of that species.

A sufficient number of specimens of *rotiforme*, however, always show all the intermediate stages between the extremely thick *latum*-like young (Plate III. Fig. 15) of one variety and a variety in which the young are difficult to separate from the adult of *kridion* by their forms and external characteristics. The

<sup>&</sup>lt;sup>1</sup> Lias Amm., pl. v. fig. 1-3.

sutures of the nearly adult *kridion* are, however, often quite distinct from those of a *rotiforme* of the same size, but whether this difference is invariable or not, I am unable to say.

The largest specimen in the Museum of Stuttgardt is 470 mm. in diameter. On the latter part of the whorl the pilæ are nearly obsolescent, with no geniculæ, thus reverting exactly to the condition of those of *Cal. Johnstoni*, var. *torus*. The sides were rounded, channels very shallow, but the keel still prominent. There is also a fragment of a very old specimen figured by Quenstedt.<sup>1</sup>

His Fig. 5, together with his Fig. 9, quoted above, show that the living chambers of the nealogic stages probably exceeded one volution in length, but we have not been able to ascertain what they were in adults.

## Coroniceras lyra, HYATT.

Plate IV. Fig. 1-17. Plate V. Fig. 1-3 a. Summ. Pl. XII. Fig. 13.

Coroniceras lyra, Hyatt, Bull. Mus. Comp. Zoöl., I., No. 5, p. 78.

Amm. multicostatus brevidorsalis, Quenst., Amm. Schwäb. Jura, pl. vi. fig. 4-6; pl. vii. fig. 1-6.

Amm. multicostatus, Hauer, Ceph. Lias d. Nordöstl. Alpen, pl. vii. fig. 7, 8 (not fig. 9, 10).

Arietites bisulcatus, Wright, Lias Amm., pl. iii., iv.

Localities. - Semur, Aalen, Filder, Gmünd, Boll, Tübingen.

## VAR. A.

#### Plate IV. Fig. 1, 8, 12-14.

This is similar to *Cor. rotiforme*. The bases of the superior lateral saddles are very narrow on the sixth or seventh whorl. The bases of the superior lateral lobes are proportionally broad, and on the same line with the geniculæ, instead of on the side, as in other varieties. The superior lateral saddles are pointed, but on the eighth whorl they become broader, and are subdivided by three marginal lobes. The abdominal lobe is longer than the superior laterals by about one third, and the inferior lateral saddles exceed in depth the superior laterals by about one fourth.

#### VAR. B.

## Plate IV. Fig. 2-5.

This has young with the same rapid lateral increase and deep pit-like umbilicus during the first whorl which was previously observed in Cor. rotiforme. The lateral increase is, however, less marked on the second whorl, and the abdomen begins to become more prominent and rounder. The pilæ began as folds, probably on the second or third quarter of this volution, and the angular ridge, which is to become the keel, appeared on the last quarter of this or the first quarter of the third volution. The pilæ never overhang, nor does the abdomen acquire greater breadth than the dorsum, as in the young of Cor. kridion and Cor. rotiforme. This stage is skipped entirely, and it is replaced by a stage having the same proportions and pilæ as in the more advanced stages of Cor. rotiforme. The abdomen on the third whorl becomes flatter, the keel plainer, and

<sup>&</sup>lt;sup>1</sup> Amm. Schwäb. Jura, pl. xv. fig. 2.

the channels are indicated by faint depressions. Upon the third quarter of this whorl continuous channel ridges appeared, flanked by tuberculated geniculæ bending forwards upon the abdomen. The flatness of the abdomen is due to the rise of the geniculæ upon the sides, which occurred previous to the appearance of the tubercles. The tuberculated geniculæ began to fall below the level of the abdomen upon the last quarter of the fourth whorl, and the abdomen became in consequence more elevated. The whorl acquired rapidly the flattened sides and peculiar aspect of the adult, and the transformation was completed on the third quarter of the fifth volution. Thus in the earlier stages there is a smooth elevated abdomen, which becomes flattened in the next stage, and then elevated again, but in the last stage it is furnished with keel, channels, and geniculæ.

The sutures on the last part of the third whorl have an abdominal lobe one third longer than the superior laterals, but the superior and inferior lateral saddles are of equal depth. These proportions are still unchanged on the first half of the fifth whorl in some specimens, whereas in others, on the last half of the same whorl, the difference between the lobes and saddles is about one fifth, and on the second quarter of the sixth volution the proportion becomes one third. Before the close of the fourth volution the lobes become more complicated and broader at the top, and the marginal saddles more numerous and leaf-like, as in the adult of their own species; the inferior lateral saddles are also deeply cut by two marginal lobes into three marginal saddles. The similar tripartite division of the superior lateral saddles and superior lateral lobes becomes at the same time very marked. The saddles also broaden out at their bases, and upon the sixth volution spread over the geniculæ. This broadening of the bases of the saddles, and the position occupied by the bases of the superior lateral lobes in consequence of this, are characteristics of some value in the species. They also show that the external characteristics of the shell develop contemporaneously with the sutures, and arrive together at their adult development upon the latter part of the fifth whorl. The abdominal lobe extends beyond the superior laterals by about one third of its own length, and the inferior lateral saddles are deeper than the superior laterals in the same proportion. The abdominal lobe of the last suture of the third volution is one third longer than the superior lateral lobes, but the two larger saddles are of equal depth. Quenstedt describes and figures all specimens from Suabia as having an abdominal lobe shorter than the superior laterals, and the superior lateral lobes pointed. This character was found in the nealogic and adult stages. The figures of the very aged forms which he calls Amm. brevidorsalis, Plate VII., would have had comparatively short abdominal lobes, to whatever species they might have belonged. Quenstedt complains of Wright for not paying attention to his distinctions, but we think Wright's figures of multicostatus show that he was right. The English specimens had long abdominal lobes, and, like French and German shells described above, are undoubtedly identical with those figured by Quenstedt in every other

<sup>&</sup>lt;sup>1</sup> For example, the huge *Cor. Bucklandi*, Amm. Schwäb. Jura, pl. ix. fig. 1, and *coronaries*, pl. xvi., of Quenstedt. Compare also the gradual decline in length of the abdominal lobe of an aged *Cor. trigonatum*, Plate VII. of this monograph.

respect. A subsequent re-examination and remeasurement of all specimens in the Museum of Comparative Zoölogy has shown that the average length of the abdominal lobe for nealogic and adult shells is considerably over one third longer than the superior laterals. The sutures also vary from the comparatively simple margins, with solid looking and very slightly indented saddles, to the extreme forms figured in our plates and by Quenstedt.

# VAR. C.

#### Plate IV. Fig. 9-11, 15, 16.

In this variety the channels are slower in reaching their full development, and the pile are not so prominent, but are more numerous and conform more closely to the shape of the whorl. The whorl is altogether flatter, and increases somewhat faster by growth than in variety B. The channels are hardly perceptible on the fourth volution, and in consequence of the smaller size and want of prominence in the geniculæ, the abdomen has at the same time more prominence than in variety B. These characteristics are more or less variable. Thus individual specimens may resemble variety A in some characters, or variety B in others. In a specimen of variety C, Plate IV. Fig. 15, 16, senile characters begin to be apparent upon the second quarter of the ninth whorl. The pilæ are still slightly tuberculated, the abdomen though much narrowed is still comparatively broad. In a specimen of variety B, at same time the abdomen had become narrow, the pilæ had lost not only the tubercles, but also the geniculæ, being in their second stage of obsolescence. A specimen in the Museum of Stuttgardt, from Göppingen, measuring 440 mm. in diameter, showed more pronounced senility. The sides were exceedingly convergent, the pilæ obsolescing, the abdomen elevated, though the channels and keel were not much changed. In another of the same diameter the channels were obsolete, the keel a low broad ridge, the pilæ reduced to broad lateral folds, and the sides very convergent. In the large specimens figured by Quenstedt,1 if the figures are accurate, the keel, channels, and lateral ridges are persistent.

In the Museum at Semur is a fine suite of specimens named Vercingetorix, Reynés. These specimens did not show senile decline as early as is usual in this species. One at the diameter of 525 mm. still retained the pilæ and the channels, though the abdomen had become much elevated. This specimen was distorted by lateral pressure, so that the transverse dorsal diameter was shorter than the abdominal.

Wright's figure <sup>2</sup> seems to be identical with this species, and the more compressed specimen figured on Plate IV. seems to be intermediate between my *Cor. lyra* and *Cor. Gnuendense*. I do not remember having seen any such forms myself, nor are any English specimens mentioned in my notes.

<sup>&</sup>lt;sup>1</sup> Amm. Schwäb. Jura, pl. vii.

<sup>&</sup>lt;sup>2</sup> Lias Amm., pl. iii.

## Coroniceras trigonatum, HYATT.

Plate VI. Fig. 3. Plate VII. Fig. 1. Summ. Pl. XII. Fig. 15.

Aster. trigonatum, Hyatt, Bull. Mus. Comp. Zoöl., I., No. 5, p. 79. Amm. Brooki, Ziet, Verst. Würt., p. 26, pl. xxvii. fig. 2. Amm. Brooki (Riesenbrooki), Quenst., Der Jura, p. 68. Amm. Crossi, Quenst., Amm. Schwäb. Jura, pl. xiv. fig. 6. Amm. nudaries, Quenst., Ibid., fig. 5?

Locality. - Aalen.

Great size is a characteristic of this species. One specimen was 380 mm. in diameter, and another measured 503 mm. Quenstedt describes one from Endingen 700 mm. in diameter.

The young were seen only from the side, but the following characters could be made out, even from this point of view. The form of the whorl in transverse section at an early stage is evidently quadragonal, since during the first four or five whorls the sides are flat and the pilæ tuberculated, as in *Cor. lyra*. After this the dorsum increases more rapidly, and the whorl gradually assumes the trigonal form. The tubercles and geniculæ become atrophied, the pilæ are merely lateral folds, and the channels very shallow by the time the shell reaches the second quarter of the sixth or seventh volution. On the eighth volution the channels are represented only by smooth inflected zones on either side of the keel.

The sutures on the latter part of the sixth or seventh whorl have abdominal lobes, which are one half longer than the superior laterals, the inferior lateral saddles one half deeper than the superior laterals. The lobes and saddles are all exceedingly broad, and the outlines very complicated. After this period the sutures degenerate, the abdominal lobe decreases in length, and the lobes and saddles, though they retain their complicated marginal inflections, become proportionally broader.

A fine suite of specimens in the Museum of Stuttgardt, from the Geometricus bed, show that the species is very similar to Cor. lyra (mullicostalus of German authors). The whorl, however, has a broader dorsum, and is larger, and the volutions are less numerous. There are also fewer and stouter pilæ at the same age than in Cor. lyra. There are two varieties included under this name. One is a smaller form, with premature development of senile whorls, etc., and has broader whorls; the other is the normal form, having slower development of the adult and senile characters, and this alone has been figured.

The more involute shells of this species are the *Anm. Riesenbrooki* of Quenstedt, and the less involute are the normal *Anm. Brooki* of most German authors.

Wright describes the Stuttgardt and Tübingen specimens, but considers them identical with *Cor. Gnuendense* and his *Arietites Crossi*,—a mistake arising from not having observed the differences in the umbilicus due to the number and shape of the whorls, which are less numerous and stouter than in *Gnuendense*. Quenstedt appears to have been led into a similar error, possibly through

<sup>&</sup>lt;sup>1</sup> Lias Amm., p. 284.

Wright's visit to his collection. Quenstedt's huge specimen, 700 mm. in diameter, noted above, is described as having the pilæ obsolescent near the termination of the last volution, and the keel as showing but little above the almost obsolete channels. This, therefore, is an extreme example of senile degeneration in the clinologic stage, but it has not yet reached the nostologic stage.

## Coroniceras Gmuendense, HYATT.

Plate V. Fig. 4-9. Plate VI. Fig. 1, 2. Summ. Pl. XII. Fig. 14.

Amm. Gmuendense, Oppel, Der Jurafor., Würt. Jahreshf., XII. p. 200.
Amm. Brooki, Ziet., Verst. Würt., pl. xxvii. fig. 2.
Aster. tenue, Hyatt, Bull. Mus. Comp. Zoöl., I. No. 5, p. 79.
Ariet. Crossi, Wright, Lias Amm., p. 283, pl. x. fig. 1, 2.
Localities. — Semur, Gmünd, Göppingen, Aalen, Aargau.

The adults of this species are readily distinguishable from Cor. lyra by the smaller size of the whorls, the characteristics of the sutures, the extreme narrowness of the abdomen as compared with the dorsum, and the broad, shallow channels. The keel is more prominent also than in Cor. lyra, and the pilæ end very abruptly with geniculæ or pseudo tubercles. This peculiarity is observable on the latter part of the sixth whorl, and the bending forward of the geniculæ, as they rise on the narrow abdomen, is hardly observable on the cast until after the completion of the seventh whorl. On the eighth volution the geniculæ become less prominent on the cast, and the depressed geniculæ and pilæ form a single arch slightly interrupted by the tubercular aspect of the former. These characteristics are not altered when the shell is present, but have about the same expression as upon the cast. The geniculæ on the seventh whorl, in one specimen examined, are prominent, and their forward bend plainly observable, though without tubercles.

The abdominal lobe is broad and deep (Plate V. Fig. 5). The superior lateral saddles and lobes are nearly obsolete, the inferior lateral lobes and the first auxiliary saddles are but slightly developed. On this account the inferior lateral saddles, which are of about the usual size, acquire remarkable prominence. We have already noticed, in variety C of *Cor. rotiforme*, a tendency towards the suppression of the superior lateral saddles, and here it is actually carried out. The marginal lobes and saddles of the superior laterals, however, remain on one specimen from Aargau, but on one from Semur only the inner of the three saddles is of noticeable size. These characteristics are present in the adults of this species, and consequently are not due to old age.

On the latter part of the eighth whorl the pilæ lose their tubercles, (Plate V. Fig. 5,) and the geniculæ become almost obsolete, being reduced to curved continuations of the depressed arched pilæ, which are most prominent at the umbilical shoulders. The channels continue to be very well defined, though much shallower, (Plate V. Figs. 8, 9,) and channel ridges are preserved until the first quarter of the tenth whorl. On the second quarter of this whorl the pilæ are

<sup>&</sup>lt;sup>1</sup> Amm. Schwäb. Jura, p. 115.

straight, prominent dorsally, but obsolete on the edge of the abdomen. The channel ridges have also disappeared, and the channels are only indicated on either side of the keel. The keel, however, is persistent.

The abdominal lobe on the latter part of the ninth volution is somewhat more than one half longer than the superior laterals, and the inferior laterals one half longer than the superior lateral lobes. This is a senile tendency to return to larval proportions, since the proportional adult difference in length of the abdominal lobe is at least three fifths.

A specimen in the Geometricus bed, from Nurtingen, labelled nodosaries, in the Museum of Stuttgardt, exhibits the characteristics of this species. Quenstedt's original of nodosaries shows that the identification of such specimens with his nodosaries is not correct. It is very often regarded as the young of Cor. trigonatum, but is far too much compressed, and whorls too small, though otherwise quite similar.

Wright's figure of an old specimen of this species under the name of Ariet. Crossi leaves little room for doubt that it occurs in England with the same peculiar form as in Germany. Wright does not mention that there are any varieties.

#### SECOND SUBSERIES.

## Coroniceras Sauzeanum, HYATT.

Plate VI. Fig. 4-14. Plate VIII. Fig. 1-3. Summ. Pl. XII. Fig. 10.

Amm. Sauzeanus, D'Orb., Terr. Jurass. Ceph., p. 304, pl. xcv. fig. 4, 5.

Amm. spinaries, Quenst., Der Jura, pl. vii. fig. 4; Amm. Schwäb. Jura, pl. ii. fig. 8-14 (fig. 15-17?).

Localities. — Whitby, Leicestershire, Semur, Salins, Gmünd.

D'Orbigny's original specimen, (Plate VI. Fig. 12, 13,) with which this identification was made, is smooth probably throughout the first four whorls. The centre was obscured, and the exact number of whorls was estimated. The abdomen is flat, with a very obscure siphonal ridge on the fifth whorl. The pilæ are terminated by a tubercle, which is elevated so that it stands on a level with or above the abdominal continuation of the pilæ. These nearly meet, and in some specimens actually do cross the siphonal ridge, giving the shell a microceran aspect.

The further development of these peculiarities would lead to a form in which the keel would become more distinct, but would be guarded by very shallow channels, and in which also the pilæ, gracefully curving as in this specimen, would terminate in a tubercle standing out prominently on the edge of a flattened abdomen. Such a form, of which the young is shown in Fig. 10, 11, occurs in the same locality, and it is evidently an older individual of this species.

The sutures of this specimen are visible on the third quarter of the sixth whorl. The abdominal lobe is shallower and broader than in variety *Gaudryi*, and the inferior lateral saddles also broader proportionately. The sutures are more like those of the young of variety A, *Cor. bisulcatum*. The edges of the

lobes and saddles are, however, serrated, not deeply divided by the marginal lobes, as in the last named species. The abdominal lobe is one half longer than the superior laterals, and the inferior lateral saddles exceed the superior laterals in the same proportion.

A fine suite of these specimens exists in the Museum of Stuttgardt, showing the variations described above. Some are very decidedly planicostan in aspect, but not more so than other specimens of Coroniceras, in which the keel becomes entirely suppressed, and the abdomen is crossed by the pilæ. Young specimens from Behla pass through stages which repeat exactly the characteristics of Corolic kridion when considerably older and perhaps full grown. One of these is labelled capraries, Fraas, planicostan variety; another lot of three specimens is named Danubicus, on account of their thick whorls and pilæ. A large specimen from Gmünd, on the last part of the last whorl, has all the characteristics of the stout English specimens of var. Gaudryi, Reynés. There is also a fragment of a much older shell, the dorso-abdominal diameter of the whorl being 60 mm., which has similar characters. The channels are, however, very broad and shallow, and the keel also low and broad.

Since the above and the description of var. Gaudryi were written, I have found in the collection of the Museum of Comparative Zoology English specimens of this species exhibiting the young. In these, for one or two volutions, the whorls are smooth, then obscure tubercles or swellings begin to appear upon the sides, which elongate into folds on the third whorl, and become distinct pilæ on the latter part of this whorl or the first quarter of the fourth. The external resemblance to the young of Cal. Johnstoni is complete in the pilæ, the compressed or embryonic form of the whorl, and the absence of a keel; the sutures, however, do not appear to be similar. Even on the early portions of the third whorl the abdominal lobe is quite long, the superior and inferior lateral lobes exceedingly short, and the corresponding saddles of equal depth. From this time the complication consists in the crenulation, or rather serration, of the margins, and the slow increase of depth in the superior lateral saddles; the other saddles and lobes remain about what they were at first with regard to their proportions. The keel is perceptible as a slightly raised siphonal line on the first quarter of the fifth whorl or last of the fourth. In the first of this stage, the abdomen, pilæ, and form of the whorls are similar to those of the adult of Cor. kridion. On the fifth volution, however, the abdomen becomes flatter, the genicular band of the pilæ more abrupt, and finally tuberculated, and the hitherto divergent or gibbous sides flatter and slightly convergent.

The young figured by Quenstedt<sup>1</sup> are questionable. They are more completely pilated than is usual in the species, and the form of the whorl is quite different. We doubt the correctness of the identification.

<sup>&</sup>lt;sup>1</sup> Amm. Schwäb. Jura, pl. xi. fig. 15-17.

### VAR. Gaudryi.

#### Plate VI. Fig. 14. Plate VIII. Figs. 1-3.

Cor. multicostatum, Hyatt, Bull. Mus. Comp. Zoöl., I., No. 5, p. 78. Amm. Gaudryi, Reynés, Plates. Ariet. Sauzeanus, Wright, Lias Amm., Pal. Soc., pl. viii. fig. 1-6.

On the sixth volution this shell has slightly convergent sides, a thick, low keel with shallow broad channels. The pilæ are tuberculated, and the geniculæ bending forward break up the channel ridges into a series of waves. They also pass over the umbilical shoulder on the dorsal side, but are not so prominent there. The very rapid increase in size of the whorl renders the umbilicus about half an inch deep at the end of the sixth volution. On third quarter of the fifth whorl the channels are very faint, the geniculæ where they ascend upon the abdomen are less prominent, and tubercles much higher up on the edge of the abdomen. If the pilæ were less prominent and devoid of abdominal extensions, this stage would precisely represent the usual form of var. Sauzeanum.

On the fifth and sixth whorls the abdominal lobe is about two fifths longer than the superior laterals, and the inferior lateral saddles exceed the superior laterals in the same proportion.

The German specimens are precisely like the English. One in Quenstedt's collection from Betzenrieth bei Göppingen is identical with the English specimen of the same age. Wright's figures all belong to var. *Gaudryi*, and exhibit a well defined keel and convergent sides at an early age.

#### Coroniceras bisulcatum, HYATT.

Plate VII. Fig. 2-10. Summ. Pl. XII. Fig. 11.

Amm. bisulcatus, Brug., Encycl. Meth., I. p. 39, pl. xiii.
Amm. bisulcatus, D'Orb., Terr. Jurass. Ceph., p. 187, pl. xliii.
Cor. bisulcatum, Hyatt, Bull. Mus. Comp. Zool., I., No. 5, p. 77.
Ariet. rotiformis, Wright, Lias Amm., p. 278, pl. ix. (not pl. v., vii.).
Amm. multicostatus, Sow., V. p. 76, pl. ceccliv.
Amm. multicostatus, Hauer, Ceph. Nordöstl. Alpen, pl. i. fig. 3, 4.
Ariet. subnodosus, Wright, Lias Amm., p. 288, pl. vi. fig. 2, 3.
Amm. resurgens? Dum., Études Pal. Bassin du Rhone, pt. 2, pl. xxiii. fig. 8-6.
Amm. multicostatus, Ziet., Verst. Würt., pl. xxvi. fig. 3.

Localities. - Lyme Regis, Semur, Hechingen, Balingen.

There are four specimens of this species, two from Semur, one from Hechingen, and one from Balingen, which differ in a significant manner. Both of those from Semur have a somewhat closer resemblance to the full grown Cor. Sauzeanum than the German specimens; they differ, however, in some respects. On one, the pilæ are visible on the last quarter of the sixth whorl, and show on the cast distinct traces of tubercles, and the geniculæ terminate before they reach the channel ridges, which are continuous and entire. In the other specimen, the pilæ are visible on the first quarter of the seventh whorl, do not show on the cast distinct traces of tubercles, and the geniculæ pass over the channel ridges as in Sauzeanum. In both German specimens the channel ridges have a crenulated

outline, and the pilæ are similar. As a whole these four specimens differ from Cor. Sauzeanum, var. Gaudryi, in having a shallower umbilicus and a somewhat greater number of whorls in proportion to the size of the shell. One specimen from Semur is intermediate in characters between the German specimens, and the true Sauzeanum, var. Gaudryi. The Semur specimens also differ in the depth and groove-like aspect of the channels, and the almost sunken aspect of the keel on the casts. The prominence of the geniculæ reminds one of the fifth whorl of Sauzeanum, var. Gaudryi.

Both specimens from Semur have similar sutures. The ventral lobe is deep, the superior lateral saddles and lobes very shallow and broad, the inferior lateral saddles very prominent, and the inferior lateral lobes obtuse. The marginal lobes are more evenly distributed than in the German variety. The sutures on the seventh whorl have an abdominal lobe from one half to two fifths longer than the superior lateral lobes, and the inferior lateral saddles exceed the superior laterals in the same proportion. Both in fact approximate to Cor. Sauzeanum, var. Gaudryi, by their sutures. In the German specimens the lobes and saddles show about the same general proportions, though the inferior lateral saddles are much broader, and the inferior lateral lobes deeper, and acute instead of obtuse. There is a large specimen in Professor Quenstedt's collection from Bodelshausen (No. 10673), which is similar to these, but unfortunately the name of this was not noted.

The keel is quite prominent at the earliest period observed on the first quarter of the fourth whorl, but the channels are hardly discernible. At this period the channel ridges are not developed, and the tuberculated geniculæ are high upon the sides. When the channel ridges are distinguishable on the fifth volution, they are continuous. The keel loses its prominence after the channels deepen upon the latter part of the fifth, and the early part of the sixth whorl. The pilæ in the young are more numerous than in the adult.

The largest specimen from Semur measured 348 mm. in diameter, and had about eight and a half volutions. The pilæ retained all their adult peculiarities and original sharpness, and the quadragonal form of the whorl was also unchanged. The channels were, however, broader and shallower than in the adult. The approximation of this form in aspect and characteristics to its morphological equivalent, *Cor. lyra*, is so close, that only the most careful study can show them to have been distinct. The young of these two species are quite different at all stages, and can generally be readily separated.

This species has always the broad abdomen of Sauzeanum and its spinous tubercles, and the young are not so stout as in Cor. lyra. In the succeeding stages the young of lyra rapidly changes from divergent to parallel sided, and then to a convergent sided whorl, whereas in this species the development is much slower. The later stages (Plate VII. Fig. 8) are similar in form to lyra when quite small (Plate IV. Fig. 9). The geniculæ usually cut up the channel ridges into waves, and, though not invariable in the species, this occurs so generally as to be a useful distinction, and is evidently of genetic importance in the series. The resemblances of the young to the adult of kridion and the young of

rotiforme may be observed by comparing the figures on Plates VII. and III., but from these it may be distinguished by the flatness of the abdomen, the elevated geniculæ, and the much earlier development of the channels.

At Semur there are several varieties of this species. One was 620 mm, in diameter, the last whorl about 170 mm, in diameter from abdomen to dorsum. The abdomen was quite narrow on the last whorl, but the tubercles were still traceable, or rather the geniculæ were very thick and prominent, resembling tuberculations. Another specimen 650 mm, in diameter, has a last whorl 240 mm, in diameter, and the abdomen much narrower, about 110 mm, in breadth, the dorsum being fully 160 mm, in breadth. The keel in this more advanced senile stage is considerably reduced in size, and the channels are almost obsolete; the tubercles are nearly obsolescent, but the geniculæ still rise above the edge of the abdomen. This peculiarity of the pilæ shows that the Sauzeanus form is persistent, and it enables the observer to distinguish the differences between a member of this series and all others.

Wright's figure <sup>1</sup> of a specimen from Semur, named by him Arietites rotiformis, looks like the full grown adults of the more discoidal variety of this species, but his reference of it to the Lower Bucklandi bed is probably incorrect. Dumortier <sup>2</sup> declares that a species identical with bisulcalus, D'Orb., but with channels not so deep, is found in several localities in the Angulatus bed in the basin of the Rhone. Unfortunately, no figures accompany his description, and figures of young and adult would be necessary to support this opinion. Cor. kridion and Verm. Conybeari are very like bisulcalum in the adults, but are quite distinct at earlier stages.

We think perhaps the more involute and broad whorled variety of this species should be recognized as distinct. It is the *Amm. resurgens* of Dumortier, and the *subnodosus* of Wright.<sup>3</sup> Wright was mistaken in placing his specimen with Amaltheus, it being an undeniable Arietian, probably occurring not later than the Obtusus bed, and perhaps as early as the Upper Bucklandi bed. In the Museum of Comparative Zoölogy there is also a magnificent specimen from Lyme Regis, measuring 375 mm. This is a perfect cast of one side, showing the same characters as in the small specimens figured by Dumortier, and the one figured by Zieten as *multicostatus*. These characters persist even at that advanced stage, without any signs of senility, and the pilæ, tubercles, geniculæ, and form of whorl remain unchanged.

The examination of Sowerby's original has induced us to join Oppel in suppressing the name of *multicostatus*. Sowerby's fossil is precisely similar to the adults of the common French variety of this species.

<sup>&</sup>lt;sup>1</sup> Lias Amm., pl. ix.

<sup>&</sup>lt;sup>2</sup> Études Pal. du Bassin du Rhone, pt. 1, p. 115, and pt. 2, p. 115.

Lias Amm., pl. vi. fig. 2, 3.

## Coroniceras Hungaricum, HYATT.

Amm. Hungaricus, HAUER, Ceph. Lias Nordöstl. Alpen, pl. iv.

The figure of this species possesses the exact form and characteristic of the bisulcatus series. It has similar unshapely geniculæ thrown out beyond the edges of the abdomen, giving the whorl a peculiar angular and squared aspect; the geniculæ also interrupt the channel ridges, and the keel, though well developed, is almost counter-sunken in the deep channels. The pilæ are very straight in Hungaricum, and have no tubercles; the form is also somewhat more compressed than in bisulcatus. The sides also are perfectly flat and parallel, and the depressed abdomen and nearly equally flattened dorsum are of the same breadth, the whorl in section being a parallelogram with the sides about one fifth longer than the transverse diameter. The specimen figured by Hauer was 135 mm. in diameter, and consequently the complete shell must have reached a much larger size, since his specimens exhibit no signs of the approach of senility.

## THIRD SUBSERIES.

## Coroniceras latum, HYATT.

Plate III. Fig. 19-23 a. Summ. Pl. XII. Fig. 16.

Coroniceras latum, Hyatt, Bull. Mus. Comp. Zoöl., I., No. 5, p. 77.

Amm. Bucklandi pinguis, Quenst., Amm. Schwäb. Jura, pl. ix. fig. 3?

Locality. - Semur.

Many of the young of this species, Plate III. Fig. 22, 23, have large tubercles early on the second whorl, and on the third these become elongated into tubercular folds. On the fourth, or on the latter part of the third volution, the intervals between them increase, and they become true pile. In other specimens, Plate III. Fig. 19, the pilæ are acquired as in rotiforme, Plate III. Fig. 5, and there is also in many specimens, Plate III. Fig. 22, a close resemblance to the adult of Cor. kridion, Plate III. Fig. 3. The keel appears on the first quarter of the fourth whorl, but at the latest stage observed on the second quarter of the fifth volution of a cast the keel was still very thin, sharp, and but slightly elevated. The channels, however, though very shallow and broad, had acquired lateral ridges. On the second whorl the breadth of the abdomen is very much increased by the development of tubercles, the sides becoming exceedingly divergent in some specimens, and the abdomen gibbous. On the fourth whorl the central area begins to become depressed, Plate III. Fig. 23, but the abdomen on either side retains its remarkable gibbosity. In correlation with this and with the narrow dorsum, the abdomen is never entirely covered by the succeeding whorls, but has an exposed border on both sides. On one specimen, Plate III. Fig. 22, 23, both the pilæ and geniculæ are double; in others, the pilæ are single and the geniculæ are double; on another, the duplication of the geniculæ ceases on the third quarter of the fourth whorl, with the exception of one single genicula on the last quarter, which is double. One cast of the second variety was very much broader

than any other observed, and the geniculæ were hardly yet perceptible on the second quarter of the fourth volution. Another cast, though nearly as broad as the last, is somewhat flattened on either side of the keel; it has prominent and immature tubercles, though the pilæ and geniculæ are still imperceptible, and the channels still undeveloped on the latter part of the fourth volution. These two specimens show the retention of nealogic form and characters. When specimens develop more rapidly, the great breadth of the abdomen begins to decrease, and true pilæ replace the tubercular folds on the fourth whorl.

The sutures in this species are peculiar in respect to the great breadth of the lobes and saddles in comparison with their length or depth, the regularity and small size of the marginal lobes, and the rotundity of the marginal saddles even in the oldest stage examined, on the second quarter of the fifth whorl. At this time the superior lateral saddles are not so deep as the inferior laterals, but in the latter part of the fourth whorl they are about even (Plate III. Fig. 23 a). The abdominal lobe exceeds the superior laterals by less than one third, and the inferior lateral lobes exceed the superior laterals in the same proportion. At the earliest period examined, the first quarter of the fourth whorl, the abdominal lobe is only about one fourth longer than the superior laterals, and the inferior lateral saddles, instead of being deeper, are about one third shallower than the superior laterals.

A splendid series of this species from the Bucklandi bed at Semur gives very remarkable variations. The young have all the variations above described, and in addition the following:—

- 1. Forms which at a comparatively early age have an abdomen and tubercles like the adult of var. *Gaudryi* of *Cor. Sauzeanum*.
- 2. Three specimens with young, having the typical broad abdomen of *latum*, but speedily changed by growth so as to resemble the young of *Cor. orbiculatum*.
- 3. One specimen has sides flattened, pilæ numerous and single, approximating to the adult *Bucklandi* in aspect.
- 4. Another has single pilæ in the young and double in the adult, just the reverse of all other specimens yet observed.
- 5. Another has the double pilæ in the young, but the sides are gibbous instead of being flat or divergent, and it then speedily acquires convergent sides, becoming similar to *Cor. rotiforme*. The abdomino-dorsal diameter is less than usual, and the increase in size more gradual than in the typical form of *Cor. latum*.

These variations and resemblances all seem to be expressions of transient tendencies, except those which approximate to *Cor. kridion* and *rotiforme*. The agreement of the young forms as shown above, and of Fig. 15 and 21, Plate III., the similarity of the sutures of the young of *rotiforme*, Plate III. Fig. 10 a, and of *latum*, Fig. 23 a, show that the differences between these forms are not great, and consist mostly in the excessive development of the broad-abdomened whorl in some varieties of *Cor. latum*. All the specimens I have seen are also of small size, and seem to be the young of some yet unknown adult form similar to *Cor. Bucklandi*. The sutures of Quenstedt's *Amm. Bucklandi pinguis* agree remarkably

well with those of *latum*, and lead us to hope that this may prove to be the adult. Certainly it is very distinct from the true *Bucklandi*, and the characteristics, so far as shown, are such as one might expect in the first senile stages of *Cor. latum*.

### Coroniceras Bucklandi, HYATT.

Plate III. Fig. 18. Summ. Pl. XII. Fig. 17.

Amm. Bucklandi, Sow., Min. Conch., II. p. 69, pl. cxxx.

Amm. Bucklandi, Ziet., Verst. Würt., pl. xxvii. fig. 1.

Amm. Bucklandi, Phill., Geol. York., p. 1, pl. xiv. fig. 13.

Ariet. Bucklandi, WRIGHT, Lias. Amm., p. 269, pl. i. fig. 1-3.

Amm. Bucklandi, Quenst., Amm. Schwäb. Jura, pl. ix. fig. 1 (not fig. 2, 3).

Amm. Bucklandi costaries, Quenst., Ibid., pl. xi. fig. 1.

Amm. solarium, QUENST., Ibid , pl. viii, fig. 1-3.

Amm. sinemuriensis, D'ORB., Terr. Jurass. Ceph., p. 303, pl. xcv. fig. 1.

Amm. sinemuriensis, QUENST., Amm. Schwäb. Jura, pl. xi. fig. 18-20.

Cor. sinemuriense, HYATT, Bull. Mus. Comp. Zool., I., No. 5, p. 78.

Localities. — Lyme Regis, Semur, Basle, Aargau, Scheppenstadt, Schaichhof, Balingen, Tübingen.

# VAR. sinemuriense.

Plate III. Fig. 18.

This has young which closely resembles the young of Cor. latum. The breadth of the abdomen, divergent sides, immature folds, and tubercles are quite similar. The folds also begin with large tubercles on the first part of the second whorl. On the third quarter of the third whorl the true pilæ begin. After this the abdomen no longer increases so fast in breadth, and finally, upon the latter part of this volution, or the beginning of the fourth, this region is hardly wider than the dorsum, and the sides flattened. On the first or second quarter of the fourth whorl the pilæ become duplicate or triplicate, and the broad, thin, abdominally projecting tubercles characteristic of this species arise. These peculiar pilæ and tubercles occur, in some specimens, intercalated with single pilæ and tuberculated geniculæ bending forward upon the abdomen. The keel on the third quarter of the third whorl was well developed, and must have appeared considerably earlier. The channels were but slightly developed on the first quarter of the fourth whorl, though they have well defined ridges, and probably began later than the keel, somewhere perhaps upon the last half of the third volution; but this could not be ascertained with certainty. One specimen from Semur had but two divided pilæ upon the third whorl; after this they remained single to the fifth volution, the last observed. D'Orbigny's figure of Amm. sinemuriensis was taken from a young individual of about five and a half whorls, in which the pilæ are all divided. This is as exceptional in the species as are the specimens without any divided pilæ.

The superior lateral saddles are much narrower than the inferior laterals. The abdominal lobe is about one half longer than the superior laterals.

A fine specimen of this species from Semur, Plate III. Fig. 18, retains the peculiar characteristics of *sinemuriense* for five and a half volutions, with a similar rate of increase, and slightly divergent or flattened sides. These sides become then more rounded, the pilæ single, parting with their tubercles; and on the eighth volution, or perhaps sooner, the whorl assumes all the characteristics of

the adult of *Cor. Bucklandi* of German authors. The pilæ are more widely separated, about six less on the eighth whorl than on the seventh; they are thick, solid, untuberculated, and the geniculæ bend abruptly and squarely forward on a level with or a trille above the channel ridges, interrupting them with very slight elevations. The abdomen is flattened, but more or less rounding between the geniculæ, and its breadth is a trille less than the dorsum, instead of being slightly broader, as in the young during the first five or six volutions. The channels sink into the abdomen, and the keel hardly shows above the lateral ridges.

The sutures on the third quarter of the eighth whorl in this specimen have an abdominal lobe about two fifths longer than the superior laterals, and the inferior lateral saddles are also two fifths deeper than the superior laterals.

A finely preserved specimen from Schaichhof agrees precisely in all its characteristics with the above, but on the first quarter of the tenth volution the inferior lateral saddles are about one third longer than the superior laterals. A specimen from Semur on the latter part of the tenth volution had an abdominal lobe about one third longer than the superior laterals. A slight rounding off of the abdomen, greater prominence of the keel, and shallowing of the channels, indicate the approach of old age in this specimen, whereas, at a corresponding age, the Schaichhof specimen still had the angular geniculæ and flattened abdomen of the adult.

The largest specimen of the *sinemuriense* variety, as shown by the young, was found in the Stuttgardt Museum. It measured about 610 mm. in diameter. There were some indications of old age, but the form of the whorl and the pilæ held their own wonderfully. There was also in the same Museum a specimen in which the pilæ had geniculæ on a level with the abdomen, and therefore very prominent, the channels excessively shallow, and keel broad and low; it was 375 mm. in diameter, and the channels had probably been deeper at earlier stages.

Of the specimens figured by Quenstedt in his "Ammoniten des Schwäbischen Jura," Bucklandi, Plate XI. Fig. 1, seems to belong to what we call true Bucklandi, as well as most of the figures of young on Plate X. The specimens figured as Amm. sinemuriensis, on Plate XI. Fig. 18–20, are doubtless the young of our Cor. Bucklandi, var. sinemuriense. These forms are not rare, but the adults must be rare, or they would not have escaped Quenstedt's attention.

#### VAR. Bucklandi.

The stout English variety of Bucklandi<sup>1</sup> is a form with much larger and fewer whorls than Bucklandi, var. sinemuriense. The adult whorls are similar in their general characteristics, but the young in the stout English variety has very much larger whorls, with thick, sparse, single pilæ, like the German specimen in the Stuttgardt Museum described above and the young forms figured by Quenstedt.

The Anm. solarium of Quenstedt is founded upon large, senile specimens, as is shown by the fragments figured.<sup>2</sup> Their sutures, the huge fold-like, smooth

<sup>&</sup>lt;sup>1</sup> Wright, Lias. Amm., pl. i. fig. 1-3.

<sup>&</sup>lt;sup>2</sup> Amm. Schwäb. Jura, pl. viii.

pilæ, and shallow channels, show this plainly. They probably belong to the typical variety of *Cor. Bucklandi*, though the evidence must be considered incomplete until the adults and young are known.

## Coroniceras orbiculatum, HYATT.

Coroniceras orbiculatum, HYATT, Bull. Mus. Comp. Zoöl., I., No. 5, p. 78.

Amm. Bucklandi macer, QUENST., Amm. Schwäb. Jura, pl. ix. fig. 2 (not fig. 1, 3); pl. x. fig. 5.

Amm. Bucklandi costosus, QUENST., Ibid., pl. x. fig. 1, 2.

Amm. Bucklandi, QUENST., Ibid., pl. xi. fig. 2 (not fig. 1).

Amm. oblongaries, QUENST., Ibid., pl. xiv. fig. 4.

Localities. - Semur, Scheppenstadt, Balingen.

The breadth and crowded aspect of the pilæ in the Scheppenstadt specimen on the fourth and fifth whorl, and the narrowness of the sides, resemble the characteristics of the same age in *Cor. Bucklandi*, var. *sinemuriense*, more than any other species of the same genus. The young whorls are much too small in all their dimensions, and the volutions too numerous for *Cor. Bucklandi*. The adult, with its prominent tubercles and with the dorsal broader than the abdominal region, shows a remarkable resemblance to *Cor. rotiforme*.

The last sutures on the ninth whorl have an even, rounded outline, due to the small size and regularity of the marginal lobes and the roundness of the marginal saddles, which are similar to those of *Cor. latum* on the fifth volution. The abdominal lobe is about one half longer than the superior laterals, the inferior lateral saddles exceed the superior laterals by about two fifths. The saddles and lobes, however, are broad and comparatively short in *Cor. latum* and in the young of other forms of Coroniceras. One specimen which is identical with this in the septal outlines shows the abdominal lobe on the eighth whorl to be one third longer than the superior laterals, and the superior lateral saddles are not quite one third longer than the inferior laterals.

One of the casts from Balingen measuring 288 mm. in diameter had about ten volutions. The increase in the transverse diameter of the whorl is more uniform and gradual than in Cor. Bucklandi, var. sinemuriense. On the latter part of the ninth whorl the pilæ show the approach of old age in the loss of their tubercles. The geniculæ also descend farther upon the sides, and are less abruptly joined to the abdomen, which therefore is more rounded and prominent than in the adult. The channels have become shallower, and finally lose their lateral ridges upon the latter half of the tenth whorl. The keel is still of considerable size, and thus acquires somewhat greater prominence than in the preceding stages. The breadth of the abdomen measured across the geniculæ is 6 mm. less than the breadth of the dorsum when measured through the umbilical shoulders on the second quarter of the tenth whorl, and 13 mm. less than on the fourth quarter of the same volution.

The abdominal lobes were not visible on the last quarter of the ninth whorl, but the inferior lateral saddles were one sixth deeper than the superior laterals. On the second quarter of the tenth whorl the abdominal lobe was one half

longer than the superior laterals, and the inferior lateral saddles were one third deeper than the superior laterals.

The young are generally identified with the young of bisulcatum in France and Germany. They resemble this species very closely, but have more divergent sides, whorls much stouter, and do not have the smooth period so fully shown in the young. They equally closely resemble in worn specimens the untuberculated variety of Verm. Conybeari, and are often, especially in large specimens, mistaken for Conybeari when the tubercles are either slightly developed or obscured. All of these resemblances, however, are merely transient, and not of the same value as the precise agreement of the younger and older stages in this species and in Bucklandi; it is in fact a more highly specialized bucklandian form, with better defined channels and smaller and finer pilæ. The resemblances in the aspect of the young to Cor. lutum are not sufficient to unite the species.

Canavari, in his Unterer Lias v. Spezia, describes and figures Cor. (Ariet.) sinemuriense, Pl. XX. Fig. 1, which may be the young of that species. Cor. (Ariet.) Monticillense, Fig. 3, 4, and rotiforme, Fig. 12, may be both the young of the last named, or of some other allied species. Ariet. mullicostatus does not resemble, so far as the lateral view given in Fig. 7 allows one to see, any species that we know.

## FIFTH, OR AGASSICERAN BRANCH.

The shells are discoidal only in the radical species and lower members of the same genetic series; in the more specialized and higher forms of the same series the involution may exceed that of the shells of any series previously described, except Schlotheimia. Thus, in shells in which the geniculæ are absent, the whorl may pass inwards beyond the area of the abdomen, and embrace the sides. The umbilicus, however, so far as observed, has never been entirely covered in. Degeneration of the form of the whorl, i. e. flattening and convergence of the sides, narrowing of the abdomen, and the advent of fold-like pilæ, may take place at an early nealogic stage in some species, and may be characteristic of entire series. The keel is, however, retained even in extreme old age. The keel takes on a distinct aspect in one series of this branch, Agassiceras, and is transitional to the true hollow keel of Oxynoticeras.<sup>2</sup>

#### AGASSICERAS.

The characteristics which distinguish this genus are principally due to the exceedingly immature aspect of the lower forms, the shortness of the living chambers, and the development in the higher species of tuberculated pilæ in association with highly convergent sides and angular keeled abdomens without channels. The young of the radical species, *Agas. lævigatum*, are remarkable for

<sup>&</sup>lt;sup>1</sup> Paleontogr., XXIX.

<sup>&</sup>lt;sup>2</sup> Quenstedt considers it to be a true hollow keel. See below, in the description of Agas. Scipionianum.

the prolonged existence of the goniatitic proportions, which are generally confined to næpionic stages of growth in other Ammonitinæ. They are also very similar in some of the nealogic and adult stages, both in form and characteristics, if we except the sutures, to Psiloceras.¹ The sutures acquire the deep arietian abdominal lobe quite early in life. The sutures of the higher species, Agassiceras Scipionianum, are very similar to those of Coroniceras. The affinities of Agas. lævigatum and Ast. obtusum, and also those with Psiloceras, have been fully discussed elsewhere.² In the clinologic stage the abdomen becomes more acute, and the sides smooth. Neumayr has lately redescribed this genus in part under the name of Cymbites.³

## Agassiceras lævigatum, HYATT.

Plate VIII. Fig. 9-14. Summ. Pl. XIII. Fig. 1.

Amm. lævigatus, Sow., Min. Conch., pl. 570, fig. 3. Amm. lævigatus, Opp., Die Juraf., p. 81.

Amm. abnorme, Hauer, Unsymm. Amm. Hierl.-Schich., Sitz Akad. Wien, XIII. pl. i. fig. 11-17. Cymbiles globosus, Geyer, Ceph. Hierl.-Schich., pl. iii. fig. 26.

Localities. -- Lyme Regis, Semur.

This species has an exceedingly immature or næpionic form. It seems frequently to complete its growth in five whorls. The aperture has a simple pointed rostrum, the lateral edges slightly flaring, with a broad shallow constriction, Pl. VIII. Fig. 12, very similar to the aperture of Oppel's type of Anm. planorbis.<sup>4</sup> The living chamber is about one half a volution in length.

- Var. A, Plate VIII. Fig. 11. This is smooth during four volutions, and the pile, if present, are developed only on the last whorl. The whorls are more compressed than in other varieties, and the umbilicus not so deep.
- Var. B, Plate VIII. Fig. 9, is smooth only during the first three or three and a half whorls, and then has immature folds like those of var. *plicatum* of *Psil. planorbe*. The younger whorls are wider than in other varieties, and the umbilicus deeper.
- Var. C has the pilæ much more distinct, but the period at which they appear is the same as in the preceding variety. The pilæ are apt to cross the abdomen, forming slight ridges. This, like all other characteristics, is found more or less also in other varieties.
- Var. D, Plate VIII. Fig. 10-12, is founded on the presence of a faintly defined siphonal ridge. This includes members of other varieties, regardless of the time at which the pilæ are developed, their greater or less prominence, and
- <sup>1</sup> A paper by E. Haug, "Ueber Polymorphidae," Neu. Jahrb. Mineral., 1887, II. p. 92, gives an interesting account of this genus, in which he substantially agrees with our descriptions, but insists upon the keelless character of the whorls. If we are correct, this is an adventitious character common enough in dwarfed forms, or arrested development in some individuals or in the varieties of the same species, but a variable within the species, and not a generic character.
  - <sup>2</sup> See pages 65, 66.
  - <sup>3</sup> Jahrb. Geol. Reichsans., XXVIII., 1878, p. 64, note.
- <sup>4</sup> We have studied Oppel's type of this species, and found that Oppel's figure gives the lateral curves of the aperture in an exaggerated form, and the constriction too deep. The real aperture is therefore more like that of lavigatum than it appears to be in his figure.

the breadth or thinness of the whorls. Some of these have stouter adult whorls than usual. If the slight siphonal ridge were absent, there would be a closer resemblance in form to Psil. planorbe, var. erugatum. The young have at first deep umbilici, due to the abrupt umbilical shoulders, Plate VIII. Fig. 10, 13, 14. common to the Goniatitinula and early næpionic stages of the Arietidæ. This stage is succeeded by flatter whorls and less abrupt umbilical shoulders, which last in some cases throughout the first three whorls, but the fourth whorl is apt to increase fast enough to be somewhat broader than the third. The aspect of the umbilicus when the fourth whorl is completed is thus altered in such specimens from deep to shallow, just as it changes at much earlier stages in other species after the earlier goniatitic proportions are outgrown. In some specimens this change takes place much earlier. The pilæ are introduced generally after the second stage of growth, and but very rarely before the reduction in the comparative breadth of the whorl begins. The sutures are also immature on the fourth whorl, but the abdominal lobe is considerably deeper than the superior laterals, as among true Arietidæ. The other lobes are pointed, and the saddles serrated.

The Museum at Semur and the Museum of Comparative Zoölogy afford ample material for tracing the connections between this species and Agas. striaries. Quenstedt, in "Ammoniten des Schwäbischen Jura," p. 106, has also noted the affinities of this species and striaries. According to Oppel, it appears in the bed immediately above the Bucklandi bed, and in the Museum of Stuttgardt is a specimen in the Geometricus bed from Degerloch. In England, however, it is usually found associated with Deroceras planicosta in the Obtusus zone, and at Semur with Schlot. angulata, and above this in the Geometricus bed. The specimens described and figured by Hauer and Geyer from the Hierlatz fauna seem to be unquestionable, since no other species with which we are acquainted has the peculiarities of this form.

## Agassiceras striaries, HYATT.

Plate IX. Fig. 14, 15. Summ. Pl. XIII. Fig. 6.

Amm. striaries, Quenst., Der Jura, p. 70, pl. viii. fig. 5. Amm. striaries, Quenst., Amm. Schwäb. Jura, p. 105, pl. xiii. fig. 24-26. Psiloceras planilaterale, Hyatt, Bull. Mus. Comp. Zool., I., No. 5, p. 73.

Sides of the whorls in adult specimens may be either flattened or decidedly gibbous, and also either plicated or smooth. Abdomen is very broad, depressed, convex, smooth or very slightly ridged by lines of growth. The position of the siphon is often indicated by a ridge. The young are smooth for the first three whorls, the plications begin to appear on the fourth whorl. These observations were made upon five specimens in the Museum of Comparative Zoölogy, which had been labelled *Amm. planorbis* by M. Boucault; but they differ from that species in the smaller size and greater proportional bulk of the whorls, the breadth and depressed convex form of the abdomen, and the presence of a siphonal ridge.

Several specimens of this species in the Stuttgardt Museum, Upper Bucklandi bed, from Balingen, showed living chambers, as pointed out to me by Professor Fraas, always much shorter than in planorbe, and the sutures distinct. The peculiar folds appearing on some shells, and the form and aspect of the whorls, like those of the nealogic stages of Scipionianus, show that their affinities are in the direction of this species. The examination of the originals of Quenstedt's descriptions from Pforen fully sustained the above, and a fine suite of the same species at Semur, in the corresponding horizon, exhibited several forms transitional to the young of Scipionianus.

Professor Mösch, in the Museum of the Polythenic at Zürich, showed me several specimens of *striaries*, in which the keel was so faint as to be hardly perceptible, and the striations no better marked than in Psiloceras. These were named *psilonotus*, and were found at Salins associated with typical *striaries*. The apertures are also similar to those of *Psil. planorbe*.

## Agassiceras Scipionianum, HYATT.

Plate VII. Fig. 11-15. Plate X. Fig. 11-13. Summ. Pl. XIII. Fig. 7.

Anm. Scipionianus, D'Orb., Terr. Jurass. Ceph., p. 207, pl. li. fig. 7, 8.

Anm. Scipionianus, Quenst., Amm. Schwäb. Jura, pl. xiv. fig. 1-3 (not pl. xvii.).

Ariet. Scipionianus, Wright, Lias Amm., p. 289, pl. xiii. fig. 1-3; pl. xix. fig. 8-10.

Localities. — Whitby, Semur, Arton in Luxemburg, Gmünd.

This species varies exceedingly. Some of the young show a crenulated keel, and they may also be either smooth or pilated on the sides. The abdomens are keeled, and occasionally, though very slightly, channelled. The form of the whorl in the young may be either very gibbous, Plate VII. Fig. 11, 12, or comparatively compressed. The pilæ also vary from comparatively thin and depressed to prominent and well defined, with or without tubercles; they may also be very numerous or few in number, and be very distinct, or thick, awkward-looking folds. It has been commonly supposed that the true affinities of this fossil were with the margaritatus group, but its development is altogether peculiar, and its sutures are distinctly arietian. There are two varieties of this species with distinct nealogic stages but similar adults; one, as described above, very gibbous and heavily pilated, and another more compressed at all stages, and approximating to Agas. nodosaries. The latter may be identical with Agas. nodosaries, or it may be distinct; the materials at hand are not sufficient to determine this question.

In old age the tubercles are suppressed, the sides become flatter and more convergent, the geniculæ bend less abruptly and curve slightly forward, the channels disappear, but the keel remains very prominent and sharp. The clinologic stage just before the pilæ become obsolete is very similar to the adult of Ast. Collenoti, but the shell is not so involute.

The young of this species has the gibbous volutions so characteristic of lævigatum and striaries. The sides are at first divergent, but they become nearly

<sup>&</sup>lt;sup>1</sup> Plate vii. fig. 11, 12; pl. x. fig. 11, 12.

<sup>&</sup>lt;sup>2</sup> Plate x. fig. 13; pl. vii. fig. 15.

parallel on the latter part of the second whorl; the dorsum also broadens, and the umbilical shoulders become more abrupt. On the third volution the sides are parallel, the dorsum and abdomen of the same breadth, and the latter elevated into an obtuse ridge. This ridge on the fourth whorl becomes a true keel, unaccompanied by channels, though there are traces of their formation. The increase of the abdomino-dorsal diameter of the whorl after this period speedily elevates the abdomen, and proportionally decreases the transverse diameter of the shell on the latter part of the fourth volution, destroying even the faint traces of the channels mentioned above. On the fifth volution the sides become slightly convergent, and this convergence increases very slowly on the sixth volution.

Thick and widely separated folds appear on the early part of the third whorl, but rapidly grow into true pile. The geniculæ may become tuberculated on the fifth volution, or they may remain permanently without tubercles; there is, however, great variation with regard to their prominence and number.

The duration of the different stages of growth also varies; in some specimens the abdomen remains flattened through the keel-forming stage until the first quarter of the fifth volution is reached. In one specimen the pilæ are reversed in position, bending posteriorly, but subsequently begin slowly to change to a natural position on the fifth volution. A number of the specimens from Semur have the pilæ but very slightly or not at all developed. None of them seem to reach beyond four and a half volutions, and their small size may possibly be due to the same cause as the absence of the pilæ.

On the early part of the fourth volution the abdominal lobe is considerably longer than the superior lateral lobes, which in turn are shorter than the inferior laterals. The inferior lateral saddles are slightly deeper than the superior laterals. On the latter part of the same volution the abdominal lobe has increased in length, and the superior lateral saddles are shallower; the inferior lateral saddles become deeper proportionally, and the lateral lobes are nearly equal in length, the inferior laterals still remaining, however, slightly the longest. The marginal lobes are very minute, and remain so, the sutures having a comparatively even outline for that reason. In some specimens the lengthening of the abdominal lobe continues until the superior lateral saddles are almost obliterated; in others, the lobes and saddles may remain with about the same proportions as in the stage of development last described.

There are two specimens in the Stuttgardt Museum, from the Geometricus bed, but they do not show the young, or give any better clue to the true development. There are also three in the Stuttgardt Museum, from the Pentacrinus bed near Krumenacher, which appear to be the young of this species, or of Scipionis. One of them, with the shell present, shows all the peculiar marks of Agas. striaries, while another, a cast, is so broad on the abdomen, and the fold-like pilæ are so prominent, that it looks remotely like the young of Cor. Sauzeanum. The three are identified as young of Cor. Sauzeanum, but the young of this last is very distinct in the sutures and other characteristics. A specimen in the collection at Semur, from the same horizon, under the name of Anm. lævi-

gatus, maintains the aspect of striuries until a late period of growth, and then develops the keel and form of Scipionianus; and there is also another fossil, which is exactly similar to the later, but still immature, stages of Scipionianus.

The keel may, perhaps, have a hollow above the siphon, such as Quenstedt describes in his "Ammoniten des Schwäbischen Jura," Plate XIV. Fig. 1, but the inner or nacreous layer does not form a partition between the interior of the shell and the interior of the keel, nor does the black layer occur above this partition, as in Oxyn. oxynotum and others, which have true hollow keels. In the specimens examined, the keel was elevated, as in Quenstedt's figure, but the siphon laid directly against the shell layers, which filled the interior of the keel, and there was no black layer.

# Agassiceras nodosaries, HYATT.

Anım. nodosaries, Quenst., Der Jura, p. 78, pl. viii. fig. 8; Amm. Schwäb. Jura, I. pl. xvii. fig. 1-3.

Locality. — Bempflingen.

The specimen of this species in the Museum of Comparative Zoölogy is less compressed than those figured by Quenstedt, but it shows that nodosaries is probably quite distinct from Scipionianus. The whorls are more compressed than in the latter, but the tubercles and pilæ are retained until a much later age. These same distinctions are, of course, still more marked when the species is compared with Scipionis. The exact horizon was not marked on our specimen. The cast measured 160 mm., and the outer whorl 60 mm., the same whorl at the beginning being somewhat less than 30 mm.; the greatest transverse diameter of the same was about 30 mm., and the least about 20 mm. Our specimen is, therefore, a trifle larger than the inner whorl of the fragment figured by Quenstedt in "Ammoniten des Schwäbischen Jura," Plate XVII. Fig. 1, at the point marked "k." It is also of about the same diameter as his abdominal view of the same whorl marked "q." The keel is also in the same condition, being coated with matrix, the geniculæ are bent and run nearly to the keel, there are no channels, and on the younger part of this whorl the keel is well preserved and prominent. Quenstedt's specimens were found in the Tuberculatus bed. It is not unlikely that the compressed variety of Agas. Scipionianum described above ought to be transferred to this species, but we have not been able to gather sufficient evidence to settle this question.

## Agassiceras Scipionis, HYATT.

Plate IX. Fig. 12, 13. Summ. Pl. XIII. Fig. 8.

Amm. Scipionianus olifex, Quenst., Amm. Schwäb. Jura, pl. xvii. fig. 7-10 (not pl. xv.).

Locality. — Semur.

The shell of this species is smooth at an early age, and quite similar to the old stages of *Scipionianus* in form and characteristics, but it is more involute. Quenstedt's figures and descriptions of his *Scipionianus olifex* appear to apply to

this species. His specimen as figured is, however, younger, and consequently less involute, the pile are without tubercles, and the general aspect similar. His shell was, according to his figure, notably more involute than *Scipionianus*, and this agrees also with a specimen in the Museum of Comparative Zoölogy. This last is larger than that figured by Quenstedt, and, though comparatively senile and quite smooth on the outer whorl, is more involute than any specimen of *Scipionianus* and has a more compressed and more acute whorl. My notes taken at the Museum at Semur say, "the *Scipionis* of Reynés is only a less involute form of *Scipionianus*," but it is probable that the specimen observed at Semur may have been exceptional, and either extremely old or a pathological example.

Geyer, in his Liass. Ceph. Hierlatz b. Hallstadt, mentions *Cymbites globosus*, Plate III. Fig. 26, a young form of *Agas. lævigatum*, as cited above, and also an *Æriet*. indet., Plate III. Fig. 13, which, if not a specimen of *Agas. Scipionianum*, is a very close ally. These are small shells, as is usual in that locality.

The Ægoc. Cocchi, Canav., Unter. Lias v. Spezia, Plate XIX. Fig. 11, may be a young specimen of Scipionianum, but we cannot venture to refer it to this genus.

#### ASTEROCERAS.

The form of the whorl is noticeably less discoidal than in the preceding series, except in Ast. obtusum. The abdomen in adults is usually narrower, the sides are flatter and more convergent, as well as broader, than is usual in Coroniceras. The involution is not limited to the abdomen, and the whorls tend to grow inwards, covering more or less of the sides. The pilæ are fold-like, bending forward on to the abdomen, and in most species smooth and without geniculæ. The young have very stout gibbous whorls with divergent sides, which become more and more convergent in the nealogic stages, and remain so throughout life. The keel is constant in all the young and adult specimens, but the channels are often very shallow, and sometimes absent.

The sutures have a deep abdominal lobe, but the lateral lobes are apt to be short and pointed, and the saddles broad. They are similar to those of Coroniceras, but the marginal lobes are rarely so long as in that genus. In old age the abdominal lobe and the lateral lobes and saddles are of about the same length, but become broader proportionally, the inferior lateral saddles become shallower, and this occurs also in many dwarf forms, which of course are prematurely degraded. These senile changes are more marked than in Coroniceras, though the old age is not otherwise noticeably different. The genus with relation to other genera of the Arietidæ is notably geratologous, or in other words the shells exhibit characteristics similar to those of the senile stages of Coroniceras, and these characteristics may be reproduced in the adult, and even in the nealogic stages. Each species and individual, however, also has a senile stage in which decline is manifested unmistakably, and during this stage the whorl becomes still more

convergent, more involute, and smoother, and the sutures more degenerate, but the keel, so far as observed, though it may become much depressed, never wholly disappears. Probably this does occur in extremely aged specimens, in what we have called the nostologic stage, but such extreme examples have not yet been seen by the author.

## FIRST SUBSERIES.

#### Asteroceras obtusum, HYATT.

Plate VIII. Fig. 4-8. Plate IX. Fig. 1. Summ. Pl. XIII. Fig. 2.

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Amm. obtusus, Sow., Min. Conch., II. p. 151, pl. clxvii.

Amm. obtusus, D'Orb., Terr. Jurass. Ceph., p. 191, pl. xliv.

Amm. obtusus, Quenst., Amm. Schwäb. Jura, p. 141, pl. xix. fig. 2, 3.

Ast. obtusus, Hyatt, Bull. Mus. Comp. Zoöl., I., No. 5, p. 79.

Ariet. obtusus, Wright, Lias Amm., p. 293, pl. xxi. fig. 1-5.

Amm. Smithi, Sow., Min. Conch., IV. p. 148, pl. cecevi.

Amm. Smithi, Quenst., Amm. Schwäb. Jura, p. 140, pl. xix. fig. 1.

Amm. Turneri, Ziet., Verst. Würt., p. 15, pl. ii. fig. 5.

Amm. Turneri, Quenst., Amm. Schwäb. Jura, p. 143, pl. xix. fig. 10-13.

Amm. stellaris, Hauer, Ceph. Lias Nordöstl. Alpen, pl. v. fig. 1-3.

Ægoc. sagittarium, Tate et Blake, Yorkshire Lias, pl. vii. fig. 2.

Ægoc. sagittarium, Wright, Lias Amm., p. 355, pl. lii. fig. 1-5; pl. lxii. A, fig. 1-6.

Ægoc. Statteri, Wright, Lias Amm., p. 374, pl. l. fig. 1-5 (not fig. 6-8).

Amm. capricostatus, Quenst., Amm. Schwäb. Jura, pl. xix. fig. 14, 15.
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Localities. — Lyme Regis, Whitby, Robin Hood's Bay, Boll, Balingen, Bempflingen, Salins, Besançon, Adnet.

## VAR. sagittarium.

A specimen from Bempflingen has pilæ, which cross the abdomen. Specimens in Quenstedt's collection from the same locality show this peculiar deformation, to which he calls attention, and compares them with sagittarium, but does not seem sure of the identification, since in another place (p. 252) he appears to admit Wright's association of sagittarium with Jamesoni. Blake states that his types came from the lower part of the Oxynotus bed, that is, from the Obtusus bed of other authors. This fact, and the obvious agreement of the sutures and pilæ with capricostatus, Quenst., and the Turneri deformation common in South Germany, and their differences when compared narrowly with Jamesoni, leave but little doubt that Wright was in error in thinking this form occurred in the Jamesoni bed, or was identical with Jamesoni. The specimens figured represent quite completely what is perhaps the most remarkable degradational series of the Lias. The resemblance of one of Wright's figures, Plate LII. Fig. 1, 2, to the forms of Wæhneroceras, especially Wæhn. latimontanum,2 is a remarkably good example of morphological equivalence.3 Others among these deformed specimens, both in England and Germany, resemble Microceras planicosta in the

<sup>&</sup>lt;sup>1</sup> Amm. Schwäb. Jura, p. 145.

<sup>&</sup>lt;sup>2</sup> Unter. Lias, Mojsis. et Neum., Beitr., II. pl. xx.

<sup>&</sup>lt;sup>8</sup> A very remarkable example of morphological equivalence caused by a wound is figured by Neumayr in his "Stämme des Thierreichs," 1889, p. 82. The shell of a keeled and channelled species has been broken on the abdomen, and beyond the wound the characteristics have changed so as to resemble those of Schlotheimia.

depressed form of the whorl, and the coarse pilæ which cross the abdomen have a similar broad, flattened aspect. The siphonal saddle, according to Wright's figures, Plate LXII. A, seems to have suffered considerable alteration from what it is in the typical form of *obtusum*. The lobes and saddles of the Bempflingen specimens have the regular differences of one half to one third in the lobes, and the abdomen is unusually broad.

There is a specimen of variety D, from Lyme Regis, in which for a short space the keel has been pressed inward and the sides ruptured. While on the recovery from this injury the abdomen retained a flattened aspect, it is about as broad as that of some forms of sagittarium, and otherwise similar. Narrow folds and furrows are noticeable crossing the abdomen, which correspond to similar small folds and furrows on the sides. The effect of the rupture is otherwise noticeable in the temporary absence of the pilæ and the greater intervals between the next two pairs of sutures. This example shows that there may be a tendency to vary in the direction of Microceras, which is produced in some specimens by disease, and in others by wounds. Such characteristics were not observed in the later stages of diseased specimens. They probably disappeared in course of growth, just as the similar characteristics of the young of Cor. Sauzeanum were suppressed in the adult stages.

The forms of this species may be divided into several varieties, according to the adult characteristics, and the slower or quicker development of the keel, channels, and form.

#### VAR. B.

This has flattened sides, pilæ not very prominent, but running nearly to the base of the keel, and the channels are very narrow as well as shallow.

#### VAR. C.

This is the normal *Turneri* of Zieten, and has the pilæ reaching nearly to the base of the keel in the nealogic stages, and perhaps in the adult. In all other characteristics, even in the prominence of the pilæ, it agrees with variety D.

## VAR. D.

## Plate IX. Fig. 1.

This is the typical form, and has well rounded, gibbous sides, prominent pilæ, broad abdomen, broad shallow channels, and a depressed keel.

#### VAR. E.

### Plate VIII. Fig. 4-8.

This is similar, but has deeper channels and a keel more prominent, narrower and more convergent sides in the adult, showing some resemblance to Ast. Turneri. Hauer's specimen of Amm. stellaris figured in "Nordöstlichen Alpen" belongs to this variety, and is not identical with the true stellare.

The pilæ may be gradually introduced by a series of plain folds, or by tubercular folds, Plate VIII. Fig. 4, 5. The whorl is smooth in specimens having the first mode of development for two and a quarter volutions. The increase is gradual, so that well defined pilæ are not produced until the last of the third or first quarter of the fourth whorl. An English specimen of variety A has large tubercles on the second quarter of the third whorl. These continue at long intervals, only about two to a quarter of a whorl. The true pilæ do not begin to appear until the third quarter of the fourth volution. Even then these are exceedingly oblique and fold-like, and, though they soon assume the aspect of true pilæ, retain their obliquity until the second quarter of the fifth volution. Another English specimen shows acceleration by developing similar tubercles on the last quarter of the second volution, and also by the development of perfect straight pilæ on the second quarter of the fourth volution. A third specimen of variety E, from Lyme Regis, has tubercles beginning on the last quarter of the second whorl, and perfect pilæ on the last part of the first quarter of the fourth volution.

#### VAR. Smithi.

The British Museum possesses a card with several young specimens of the variety Smithi, which at first appear to be identical with the full grown lævigatum or striaries. They have short living chambers, becoming more or less contracted at the apertures, and fold-like pilæ with striations. They have not, however, the peculiar form of the young of lævigatum, Plate VIII. Fig. 10, 13, nor similar sutural digitations, and the living chamber is about three fourths of a volution in length. It is interesting to note here the fact, that acceleration in the development of the tubercles and pilæ occurs in variety E, which has more involute shells than other varieties.

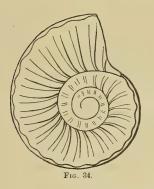
Ast. obtusum has characteristic sutures, and the number of specimens usually exhibiting these parts were also favorable for testing the diagnostic value of the proportions of the lobes and saddles in the definition of the species. We have made large numbers of measurements, of which the following are selections. The fractions express the differences between the abdominal and superior lateral lobes, or the inferior and superior lateral saddles. The abdominal lobe and inferior lateral saddles being always longer, the fraction expresses at the same time the proportionate lengths in equal divisions of these two.

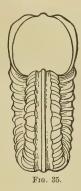
A specimen of variety B, from Robin Hood's Bay, has three sutures on the third and two on the fourth quarter of the fifth volution, with a difference of only two fifths between lobes and saddles, and one septum on the third quarter, in which the lobes are equal, the saddles remaining unchanged. One from Teuchsloch bei Bempflingen has lobes varying from one fifth to one third, and saddles from one sixth to two thirds. A specimen of variety C, from Boll, has these proportions in none of its sutures, but either two fifths or one half between the lobes, and one fifth or one third between the saddles. Comparisons were made upon sutures of the same age in each case. Another specimen of this variety from Boll, having similar gibbous sides, has similar proportions between the lobes and saddles, with exception of the eighth suture, in which the difference

of the lobes is only two fifths, and that between the cells only one fourth. This shows that the proportions in stouter specimens from Boll are not due to the greater prominence of the pilæ and gibbosity of the sides, nor is there any marked deviation from the usual rounded outline of either lobes or saddles. A specimen of variety D, from Lyme Regis, has sutures with lobes differing one half with great uniformity, but saddles differing one half to one third or one fourth, irrespective of this constancy between the lobes. A specimen from Lyme Regis shows that there is no correlation between these proportions and the variations in outline of the inferior lateral saddles. Thus, in the Lyme Regis specimens, No. 1 has the inferior lateral saddles flattened and rounded; No. 2, pyramidal, with two marginal saddles forming a club-shaped expansion at the top; No. 4, straight sides and slightly concave base; No. 5, like No. 1 again; and No. 7, like No. 4.

The sutures of the first specimen described from Bempflingen as having the microceran pile, have the usual proportions of others. A specimen from Lyme Regis has lobes differing from one half to three fifths, the saddles, however, with remarkable constancy, remaining about one half, as far as measured. The wounded specimen described above had lobes and saddles, varying from one half to the excessive difference of five sevenths, and the extremes of difference were not the nearest to the fractured portion of the shell, but some sutures removed from the fracture. A small specimen from Whitby, on the third quarter of the fourth volution, showed lobes differing from one half to three fifths, and saddles from nearly equal to one third. A somewhat larger specimen from Lyme Regis had lobes differing three fourths, and the saddles three fourths and two thirds on the first quarter of the sixth volution. On the right side of a specimen from Lyme Regis a rare distortion occurs. The first auxiliary lobes are obsolete, or at any rate only represented by a marginal lobe, and the first and second auxiliary saddles form a solid bank.

By combining all of these observations, it becomes possible to trace a series of modifications. There is evidently (1) a very immature form or variety, in which a microceran aspect is assumed through pathological causes; (2) a variety in which a low keel, very shallow narrow channels, flat sides, and depressed pilæ are developed much more quickly than in this malformed variety; (3) a variety in which the development of pilæ, channels, and keel is still more accelerated, and combined with more gibbous sides and more prominent pilæ in adults; (4) a variety in which development of the pilæ is accelerated, accompanied by the advent of broader and deeper channels, and a more prominent keel in the later stages. The specimens from Salins and Besançon are dwarfs, having resemblances to Twineri, Ziet.





VAR. quadragonatum, HYATT.

Localities. - Lyme Regis, Semur.

A form in the Museum of Comparative Zoölogy, represented in Figures 34, 35, closely resembles the stout variety of obtusum, but exaggerates the characters of that form and of variety B. Though young, it has a more subquadragonal whorl than is usual in the adults of obtusum, var. B, a flatter abdomen and broader channels, and quite distinct pilæ, with a tendency to the formation of tuberculated geniculæ, though actual tubercles are not present. The diameter is 53 mm. The outer whorl is 20 mm. on the sides, and the transverse diameter the same. The sides are about parallel, the abdomen flat, distinct, sub-angular, and geniculæ are present. The abdominal part of the pilæ do not bend forward, but pass on to the abdomen and interrupt the channel ridges. The ridges are well marked, though not so prominent as in Turneri.

It is evidently a modified form of *obtusum*, in which the pilæ by a very slight increase in the geniculæ would become tuberculated. Dumortier, in his "Études Pal. Bassin du Rhone," describes a specimen of *obtusum* having eight or nine irregular nodes upon the young whorls until 20 mm. in diameter, and gives these as characteristic of the young of his specimens. They probably belonged to this variety, in which the young are more strongly marked in this way than is usual in other varieties of *obtusum*.<sup>1</sup>

There is a large specimen in the Museum of Comparative Zoölogy, from Lyme Regis, 500 mm. in diameter. Though considerably altered by pressure, the last whorl has the aspect of var. quadragonatum, and the normal form is comparatively slightly altered on the third quarter of this volution. It is here only 115 mm. in abdomino-dorsal diameter, which is considerably less than would occur in any equally large specimen of other varieties. There are pseudo tubercles on the outer whorl, but these may in large part be due to distortion of the pilæ by

<sup>1</sup> The similarity of Arietites stellæformis, as figured by Wähner, Unter. Lias, VI. pl. xxv., to Asteroceras may be simply a case of parallelism, due to clinologic degeneration in some species, which may, however, belong to an entirely different genus. The umbilical whorls are heavily though sparsely tuberculated, and the outer whorls are, in our opinion, those of an old shell. See also page 100, note 3, above.

pressure. The keel is low and broad, as in obtusum, though prominent enough to show above the lateral ridges when seen from the side. D'Orbigny's figure of obtusum is correct, and gives this variety as it occurs at Semur, the abdomen sometimes being wider than the dorsum, instead of being narrower than or about equal to the dorsum, as in all other varieties.

There is a normal specimen of this species in the Museum at Stuttgardt, collected in the Upper Bucklandi bed at Göppingen. The majority of specimens, however, belong to the Obtusus bed just above this.

Confusion, as remarked above, is not infrequently occasioned by the resemblances of the senile stages in Cor. Bucklandi to the adults of obtusum and Brooki. Sometimes even old specimens of Cor. trigonatum and Gnuendense are mistaken by paleontolongists of experience and reputation for obtusum, especially if the inner whorls are concealed. The larger and older specimens of obtusum are apt to acquire the more abrupt umbilical shoulders which are characteristic of the young and adult of Ast. stellare.

# Asteroceras stellare, HYATT.

Plate IX. Fig. 2, 3. Plate X. Fig. 1, 2.

Amm. stellaris, Sow., Min. Conch., I. p. 211, pl. xciii.

Amm. stellaris, Ziet., Verst. Würt., p. 15, pl. ii. fig. 5.

Amm. Brooki, Quenst., Amm. Schwäb. Jura, p. 116, pl. xv. fig. 2, 3 (not pl. xx., xxi.).

Ariet. Brooki, WRIGHT, Lias Amm., p. 295, pl. xxii. fig. 1-6.

Amm. obtusus suevicus, QUENST., Amm. Schwäb. Jura, pl. xx. fig. 1.

Localities. - Semur, Lyme Regis, Gmünd, Tübingen.

The nealogic stages are similar to the older ephebolic stages of var. E of Ast. obtusum. In point of fact, the two forms run into each other by intermediate varieties, and can be separated only by artificial lines. The young in one specimen from Whitby exhibited on the first quarter of the fifth volution channels as deep, keel as prominent, and an abdomen considerably narrower than those of the most highly modified forms of Ast. obtusum, var. E, on the last quarter of the sixth whorl, over a whorl and a half later. In a specimen from Lyme Regis the development is parallel with that of obtusum, var. E, until the first quarter of the sixth whorl, then the sides became flattened, the pilæ depressed, and the abdomen narrowed to the area of the channel ridges.

Sowerby's types, figured by Wright, are young specimens, and exhibit very completely the fact that the young may develop the characteristics of the species at a comparatively early stage, and are more highly modified as a rule than the adults of *obtusum* in any variety.

The sutures on the sixth volution of a specimen from Gmünd had lobes differing two thirds and saddles one half; and on last quarter of same, the lobes differed three fourths and saddles two thirds. In an older specimen from Semur, on the second quarter of the seventh whorl degeneration had already begun, the lobes differing only one fifth to one sixth, and saddles about two fifths. This and the fold-like character of the pilæ and trigonal form showed that old age had fully begun on this whorl. There are two specimens of stellare in the Museum of Com-

parative Zoölogy, which are so similar to Ast. Turneri that they differ in only one characteristic, namely, the shallowness of the umbilicus, due to the gradual curvature of the sides. In Ast. Turneri the breadth of the dorsum, and the consequent abruptness of the umbilical shoulders, is a marked peculiarity, even at an early nealogic stage. These specimens were in the nealogic stage; if older, they would probably also have shown a less amount of involution than in Ast. Turneri. This last species becomes generally, though not invariably, larger in five volutions than the former in the course of five and a half. Specimens of stellare also approximate very closely to Ast. acceleratum; they differ, however, in the less involution of the whorls, and in other correlative characteristics.

Depressed tubercles similar to those of the young of *obtusum* appeared, in the only specimen in which they could be detected, on the last quarter of the second whorl, and true pilæ on the third quarter of the third whorl, earlier by one volution than in var. E of *obtusum*. Thus even in this unimportant character acceleration appears to have taken place as it had in other characters.

There is one specimen of this species in the Museum of Stuttgardt, from the Geometricus bed of Göppingen, though it is more common in the Obtusus bed. The largest specimen in this Museum reached a diameter of 450 mm. (Pl. X. Fig. 1, 2). The last whorl was perfectly smooth, the abdomen had become subacute, and the channels obsolescent, resembling those of the adults of Asl. Collenoti.

# Asteroceras acceleratum, HYATT.

Plate IX. Fig. 4. Plate X. Fig. 3.

Locality. - Semur.

The involution covers two fifths of the sides on the sixth whorl, and one half of the second quarter of the eighth, whereas in Ast. stellare the extreme limit of involution is one third. The whorl is similar to that of this species, but is much broader abdomino-dorsally. The umbilical shoulders are large and abrupt, the dorsum much broader than the abdomen, the latter being but little wider than the area of the channels. The latter are very broad and shallow, with smooth but depressed lateral ridges. The keel is well marked, but depressed as in obtusum. The abdomen is therefore quite different from that of either Brooki or Turneri.

The young are similar to stellare until a late nealogic stage, and differ only in the greater involution of the whorls in later stages, and in the earlier development of the senile folds and trigonal form. The umbilicus could be observed in only one specimen. In this the pilæ began with coarse folds on the last quarter of the second whorl, which developed into true pilæ on the first quarter of the fifth whorl.

The largest specimen from Semur measured 202 mm., and had completed the seventh, and part of the eighth volution. The breadth of the first quarter of the eighth whorl measured on the sides was 77 mm. There is a specimen in the Museum of Stuttgardt, labelled *Amm. stellaris*, found at Göppingen in the

Geometricus bed, and one, broken across, from the Obtusus bed at Balingen. The last (Pl. X. Fig. 3) shows the young with shallower channels and flattened sides, somewhat similar to Ast. obtusum at an older period. The sides of the young, however, are flatter and broader than I have yet seen in any variety of stellare, and more like those of an aged Cor. trigonatum. The characteristics of the nealogic stages and of the adult are evidently geratologous. This specimen is 258 mm. in diameter. The whorl of the adult is smooth, and of same shape as the senile stage of Ast. obtusum, and the sutures also agree exactly with those of the old of that species. Comparing it with a specimen of Turneri from Endigen of about the same size, it is seen that the latter has a much broader abdomen, deeper channels, more trenchant keel, and keeps its pilæ and form intact until a much later age, than Ast. acceleratum, and it does not increase in size so fast, is not so involute, and grows much larger. There are also several very fine specimens from Endigen, which enable us to connect acceleratum with stellare without the aid of the similar varieties from Semur or Gmünd, and they are regarded as so connected by Professor Fraas, who has labelled them Amm. obtusus. There is a series of five perfect specimens belonging to the Stuttgardt Museum, sufficient to convince the most sceptical. Nevertheless, it differs in the form of the young and in the adult from either stellare or obtusum, being both more involute and more accelerated in its mode of development. It is, as a rule, identified with Brooki, and it bears the same relation to obtusum that Ast. impendens bears to Turneri.

#### SECOND SUBSERIES.

### Asteroceras Turneri, HYATT.

Plate IX. Fig. 8, 9. Summ. Pl. XIII. Fig. 3.

Amm. Turneri, Sow., Min. Conch., V. p. 75, pl. cccclii.
Aster. stellure, Hyatt, Bull. Mus. Comp. Zoöl., I., No. V. p. 80.
Amm. compressaries, Quenst., Amm. Schwäb. Jura, p. 126, pl. xvii. fig. 4-6.
Amm. cf. obtusus, Quenst., Ibid., p. 143, pl. xix. fig. 9.
Amm. undaries, Quenst., Ibid., p. 148, pl. xx. fig. 2-6.
Amm. Turneri, Quenst., Ibid., p. 142, pl. xix. fig. 5 (not fig. 6-8).
Arielites Turneri, Wright, Lias Amm., p. 292, pl. xii. fig. 1-6.

Localities. - Lyme Regis, Gloucester, Semur.

The amount of involution on the third quarter of the sixth whorl is two fifths of the side. The abdomen is broader, the channels more deeply sunken and broader, and the keel thinner and less immature in its aspect, than in Ast. stellare or Ast. acceleratum. The sides also are flatter, and the dorsum is but very slightly broader than the abdomen. The umbilical shoulders are abrupt, but the umbilicus is hardly so deep as in acceleratum, the lateral increase of the shoulders by growth being considerably less than in that species, though greater than in typical varieties of obtusum. The pilæ are thinner, more numerous, and do not have the

<sup>&</sup>lt;sup>1</sup> This figure is erroneous in one important particular. The youngest part of the abdomen visible in the figure, as seen from the front, is much flattened, whereas in the specimen it was but slightly more depressed than in the older part of the same whorl, represented as trigonal immediately below.

fold-like character common in those species. They are more acute and about equally prominent near the dorsum, and also on the edge of the abdomen, and often interrupt the channel ridges. The earliest period examined was the third quarter of the fifth whorl. One specimen, from Lyme Regis, had a much narrower channel area than in obtusum of the same age, and the pilæ reached nearly to the base of the keel; in another, from Gloucester, the channels were better developed, but extremely narrow. This species even on the fifth volution had a better developed keel, deeper and more distinctly marked channels, and flatter sides, than any variety of Ast. obtusum, stellare, or acceleratum.

One specimen from Semur on the second quarter of the sixth whorl had lobes differing from two fifths to three fifths, and saddles from two fifths to

one half.

Senile characteristics begin to appear on the latter part of the seventh whorl. The pilæ diminish to large folds on the second quarter of the eighth whorl, and subsequently disappear altogether. The channels also increase in breadth and diminish in depth. The keel acquires greater prominence in the clinologic stage on account of the shallowness of the channels, but finally becomes depressed. The largest specimen measured had about eight whorls, and the diameter was 327 mm.

A fine series of this species is in the Museum of Stuttgardt. These shells became smooth at variable ages. One from Balingen, about 113 mm. in diameter, had become entirely smooth; another from Endigen nearly half a whorl older had still very prominent pilæ. The peculiar form of the whorl, the deep channels and flat sides, hold constantly, however, in these, as well as in a young specimen from Balingen, labelled *Amm. obtusus*, which also belongs to this species. This last is beautifully preserved, and may be compared with *obtusum* of the same age and perfection.

The forms identified by Oppel in the Museum at Munich as Amm. Turneri

precisely accord with the above.

The adult specimens of one variety of *Turneri* and a large variety of *Arn. ceras*, found together in the Planicosta bed at Lyme Regis, are quite similar, and have led to confusion in names, though the young are distinct, and the pilæ of Arnioceras are not bent or curved as in *Ast. Turneri*. The same error has been also repeated by Quenstedt in his identification of *Amm. cf. obtusus*, a variety of *ceras* from Ofterdingen, with the English form of this species as figured by Wright, i. e. with the young as shown in Wright's plate.

Another source of confusion lies in the resemblances of fragments of the more discoidal variety of this species, when of considerable size, to Ver. Conybeari. One fragment of an outer whorl from Lyme Regis in the Museum of Comparative Zoölogy is very similar to a Conybeari of the same size. It has pilæ not quite so straight, the geniculæ form an even curve with the pilæ, and the abdomino-dorsal diameter is greater in proportion than is common in that species.

The abdomen is precisely similar in its keel and channels.

#### Asteroceras Brooki, HYATT.

Plate IX. Fig. 5-7. Summ. Pl. XIII, Fig. 4.

Amm. Brooki, Sow., Min. Conch., H. p. 203, pl. exc. Amm. Brooki, Quenst., Amm. Schwäb. Jura, pl. xx. fig. 11, 12; pl. xxi. fig. 1 (not pl. xv.). Ariet. Brooki, Wright, Lias Amm., p. 280, pl. vi. fig. 4, 5.

Localities. - Lyme Regis, Bempflingen?

The pilæ are very close together and well defined on the first quarter of the third volution. On the last quarter of the sixth volution, peculiar geniculæ are formed by the abrupt bending of the straight pilæ, which contrast forcibly with the more gradual curves of these parts in Ast. Turneri. On the first quarter of the sixth whorl these are even better marked, owing to the depression of the abdominal parts and greater distance of the geniculæ from the channel ridges. There are, however, specimens in both species which do not differ in their pilæ at any stage, and are precisely intermediate in all characteristics (Plate IX. Fig. 5–7). The channels are perfectly well defined, and the lateral ridges are entire. The channels broaden out rapidly on the latter part of the fifth whorl, but do not increase perceptibly in depth, and have probably already reached their full adult development.

The differences between the young of this species and the young of Ast. Turneri are considerable. The young of the latter throughout the fifth volution had a whorl with a dorso-abdominal diameter but very little longer than the transverse, while at a still later stage and in the adult the dorso-abdominal diameter is two sevenths longer than the transverse. This last is about the proportion of the same diameter upon the first quarter of the fifth whorl in the young of Ast. Brooki. The sides begin to be convergent at a much earlier age in Brooki, and the resemblance to the old of Turneri becomes very close. The amount of involution is also one half on the latter part of the fifth whorl and the early part of the sixth volution, while in Turneri of the same age it is only one fourth, — about the same as in the young of Brooki.

The pilæ retain their distinctness and the channels increase in depth and breadth by growth, while the abdomen remains throughout much narrower than in Ast. Turneri. The increase of the dorso-abdominal diameter of the whorl by growth is more rapid in proportion to the transverse than in Turneri. The old shell even on the first half of the eighth whorl envelops more than half of the preceding whorl. This contrasts very decidedly with Turneri, which at the same age is less involute, and the transverse diameter of the whorl near the dorsum is but little shorter than the sides, the breadth of the abdomen being only about two fifths less than that of the sides. In this species the dorsal diameter is nearly a third less than the breadth of the sides, and the breadth of the abdomen is two thirds less.

The largest specimen measured had seven and a half volutions, and the diameter was 241 mm.

In the Museum of Stuttgardt from the Obtusus bed there is one specimen of this species labelled *Amm. Turneri*, Sow., Pleinsbach, No. 4187.

# Asteroceras impendens, HYATT.

Plate X. Fig. 6-9.

Ariet. impendens, WRIGHT, Lias Amm., p. 302, pl. xxii. A, fig. 1-5.
Ariet. Collenoti, Ibid., p. 304, pl. xxii. A, fig. 6-9; pl. xxii. B, fig. 1-3.
Amm. Fowleri, BUCKM., Murch. Geol. Cheltenh., pl. xii. fig. 7.
Amm. impendens, QUENST., Amm. Schwäb. Jura, p. 151, pl. xx. fig. 7-10.
Ariet. impendens, BLAKE, Yorkshire Lias, pl. vi. fig. 7.

Localities. - Semur, Lyme Regis.

This species differs from *Brooki* in the greater amount of the involution, the smaller size, the earlier age at which the same form of whorl is passed through, and the earlier age at which degeneration begins.

In Wright's "Lias Ammonites" the figures of Brooki, impendens, and Collenoti show in the clearest manner what are the proper limits of the species. The figure of Brooki, on Plate VI. Fig. 4, is taken from the less involute form, which retains its pilæ until a late stage of growth; that of Collenoti on Plate XXII. B is an old and very large individual of impendens, which approximates to Brooki, but has the usual difference in the amount of involution and begins to show degeneration of the pilæ also earlier than is common in Brooki; that of Collenoti on Plate XXII. A, Fig. 6–8, is a yet more accelerated form, growing old and losing pilæ, etc. earlier than in the specimen shown on Plate XXII. B. The figure of impendens itself is still more accelerated than the specimen figured on Plate XXII. A, Fig. 6–8, and has also somewhat stouter whorls. The young figured on Plate XXII. A, Fig. 4, is similar to the adult of the true Ast. Brooki, having the same form, pilæ, and involution until a late nealogic stage.

All of these forms have the broad abdomen, the peculiar channels, and the young like *Brooki*, and are quite distinct from the true *Ast. Collenoti*. They are undoubtedly transitional forms connecting the two species. Those who wish may join them, but, as we have previously said, all the series and about all the species of the Arietidæ are closely connected by intermediate forms and modifications, and, to be really consistent, we must then also include the entire family under a single specific name. We doubt if any paleontologist would secure serious support if he attempted to do this.

#### Asteroceras denotatum, HYATT.

Ann. denotatus, Simps., Foss. Yorkshire Lias, p. 76.

Ariet. denotatus, Wright, Lias Amm., pl. vi. fig. 1 (Collenoti in the text, p. 304).

Ann. tenellus, Simps., Foss. Yorkshire Lias, p. 97?

This species has been universally placed either with *Brooki* or *Collenoti*. It is, however, quite distinct from either of these forms. If one compares the figure of *denotatus* by Wright with the young of *impendens* figured by the same author on Plate XXII. A, Fig. 4, and that of the young of the same species by Quenstedt, Amm. Schwäb. Jura, Plate XX. Fig. 8, it will be seen that *denotatus* stands just between *impendens* and *Collenoti*. The young of *impendens* is much less involute, and shows the same stout whorl as in the adult, a form which is in strong con-

trast with the greater involution and flatness of the shell of denotatus. On the other hand, denotatus as figured by Wright, when compared with the accurate figure of adult Collenoti by D'Orbigny and of the young by Dumortier, shows that the latter is a form which is smooth, acute, and geratologous to an extreme degree at a much earlier age than either denotatus or impendens.

#### Asteroceras Collenoti, HYATT.

Plate IX. Fig. 10-11 b. Plate X. Fig. 10. Summ. Pl. XIII. Fig. 5.

Amm. Collenoti, D'Orb., Terr. Jurass., I. p. 395, pl. xcv.
Aster. Collenoti, Hyatt, Bull. Mus. Comp. Zoöl., I., No. 5, p. 80.
Amm. Cluniacensis, Dumort, Étud. Pal. Bassin du Rhone, p. 148, pl. xxv. fig. 8-10.
Ægoc. Slatteri, Wright, Lias Amm., p. 374, pl. l. fig. 6-8 (not fig. 1-5).

Localities. — St. Thibault, Semur.

D'Orbigny's two original specimens now in the Museum of Comparative Zoölogy show that his figures are faithful. The pilæ in a specimen from St. Thibault, figured on Plate IX. Fig. 10-11 of this memoir, arise as lateral folds on the last quarter of the second volution, and become fully developed on the third whorl. On the first quarter of the third whorl, the keel appears, and on the second quarter the channels, but these are at first only linear depressions. At this stage the involution is about one third. On the second quarter of the fourth whorl, the channels are still shallow, but have depressed, lateral, entire ridges, the pile being prominent near the dorsum and disappearing on the edge of the abdomen before reaching the channel ridges. The involution is now about one half. The transition from the rounded whorl of the early nealogic stage to the acute form characteristic of the species takes place with extraordinary rapidity during the first quarter of the third volution. The usual intermediate stage, common in other species having a quadragonal or stout whorl with more or less depressed abdomen and flattened parallel sides, is entirely omitted. During the fourth whorl the smooth inflected zones, which represent the channels in this species, become developed, and the pilæ are better defined. On the first quarter of the fifth volution the elevation and sharpness of the abdomen increase, but no obvious changes occur in other characters; the involution of the whorl exceeds one half of the side of the preceding whorl. At this stage and immediately preceding it the resemblance to the adult of denotatus is extremely close, except of course as regards the difference of size and the superior sharpness of the abdomen. On the last part of fifth volution degenerative changes begin, the pilæ rapidly disappear, and the channel zones become less distinct.1

In D'Orbigny's other specimen, from Champlony near Semur, the pilæ are equally obsolescent on the last part of the third whorl, and on the first quarter of the fourth they are represented but faintly on the sides.

In another specimen, figured on Plate X. Fig. 10,<sup>2</sup> from the same locality, the pilæ are entirely absent, being represented only by lines of shell growth, or hardly perceptible folds, even on the first part of the fifth volution. On the

<sup>&</sup>lt;sup>1</sup> Figured by D'Orbigny, Terr. Jurass., pl. xcv. fig. 6, 7.

<sup>&</sup>lt;sup>2</sup> Also figured by the same author on pl. xcv. fig. 8.

second quarter of the fifth whorl in the St. Thibault specimen, the channel ridges are still raised lines marking the angular junctions of the sides and smooth channel areas. On the last part of the same whorl in the third specimen just mentioned, and in fact on the second quarter, even this angularity has almost wholly disappeared, the channels being obsolete, the keel therefore additionally prominent. The involution of the last part of the fifth whorl covers three fourths of the sides of the preceding whorl, exclusive of the channel area and the keel, which would somewhat increase this amount.

Oppel refers this species to the young of *Guibalianus*, our *Oxyn. Greenoughi*, in which, however, he was probably mistaken. The specimens in our possession show that this species has not been correctly quoted as coming from any other localities than Côte d'Or, the basin of the Rhone, and perhaps Hierlatz.

Sutures of the first specimen described above on the third quarter of the fourth whorl had lobes differing from one third to one half, and saddles about one third; and the third specimen on the first quarter of the fifth whorl had lobes differing one third and saddles a trifle less. The outlines of the suture are similar to those of Coroniceras and Asteroceras. Three saddles are to be seen upon the side, the inferior laterals being deeper than the superior laterals, as in other species, but the first auxiliaries are unusually large, nearly as deep as the inferior laterals, and very broad. The abdominal lobe, as stated, is from one half to one third longer than the superior laterals, and the superior lateral saddles about one third shorter than the inferior laterals. There is therefore no ground for the reference of this species to the genus Amaltheus, as has been supposed by some authors. According to Oppel this species is found in the Tuberculatus bed, and though Oppel probably never saw a true Collenoti, this statement is approximately correct. Dumortier's specimens of Collenoti (Cluniacensis) were found in his Planicosta bed immediately above the Oxynotus bed, and all of his beds above the Bucklandi and Davidsoni (Striaries) beds are equivalents of the Birchii or Tuberculatus zone at Semur. D'Orbigny's originals were reported as coming from the Gryphea arcuta beds, but this was evidently considered to be doubtful by Oppel, even before Dumortier found his specimens.

The extraordinary series figured and described by Wright from the Oxynotus bed, under the name of *Slatteri*, are widely distinct. The figures of the shell and sutures we have quoted above are certainly taken from a species which is very closely allied with the true *Collenoti*. It is assuredly an Arietian, with affinities allying it to *obtusum*, and comes nearer to *Collenoti* than any other species in respect to involution, smoothness, form of whorl, and abdomen. The other members of *Slatteri* as figured are probably diseased specimens of *obtusum*.

The keel of this species was examined very carefully to determine whether it was solid or hollow, and it was found to be solid.

A dwarf form of Ast. (Ariet.) stellare is figured by Geyer in his "Lias. Ceph. d. Hierlatz b. Hallstadt," and his Ast. (Oxyn.) Collenoti is certainly very similar to, if not identical with, the French form of that name. Asteroceras (Ariet.) stellæforme, Wäh., Mojsis. et Neum., Beitr., VI., Plate XXVI., seems to be a species of this

group occurring in the Kammerkahr Alps. The young being heavily tuberculated and the pike inclined towards the apex, the umbilicus reminds one of Ast. obtusum, var. quadragonatum. If it should prove identical when the young are examined, it would be interesting as showing the early occurrence of this species.<sup>1</sup>

#### SIXTH, OR OXYNOTICERAN BRANCH.

#### OXYNOTICERAS.

This genus was formerly considered by the author as a distinct family <sup>2</sup> from the Arietidæ. The similarity of the adult sutures, their mode of development, and the affinities of Oxynoticeras with Agassiceras, which it has been possible to trace more fully since the publication of Dumortier's "Études Pal. du Bassin du Rhone," show that the genus belongs properly to the Arietidæ, notwithstanding the hollow keel. The earlier nealogic stages have the psiloceran form, and the later nealogic stages have the form and characteristics of Agass. striaries, while the adult sutures are unquestionably arietian.

Baron Schwartz, to whom we are indebted for being made aware of the importance of the hollow character of the keel among the Ammonitinæ, was at the time of our visit at Tübingen searching for specimens of Oxyn. oxynotum in which the structure of the keel could be studied. Several specimens were subsequently found by the author in the collections at Stuttgardt and Semur, which showed the essentially hollow interior of the keel in oxynotum, and also in Greenoughi, Guibali, and Lotharingum. The late stage of growth at which it appears, and the early senile stage in which it completely disappears, are very marked in Guibali, and especially in Lotharingum.

The young of Oxyn. Greenoughi and Guibali are very similar in several varieties to those of Agas. striaries, and in oxynotum they are almost identical with this species.<sup>3</sup> The young of Lotharingum, however, have more accelerated development, and skip these striaries-like forms, beginning at a very early stage to resemble the adult of Greenoughi.

These facts appear to justify the conclusion that the first appearance of the hollow keel occurred in a genus whose origin is traceable by developmental characteristics to the arietian species Agus. striaries, and whatever its subsequent value, whether characteristic of families or common to larger groups, it must be here considered as of generic importance, and certainly not sufficient to outweigh other characters, which bind the oxynoticeran series to their associates among the Arietidæ of the Lower Lias.<sup>4</sup>

Oxyn. Greenoughi is in every way very nearly allied to oxynotum, and some varieties, especially among the German forms in the Museum of Stuttgardt, have more acute abdomens than the true Greenoughi, approximating very closely to the

<sup>&</sup>lt;sup>1</sup> See notes on pages 100 and 205.

<sup>&</sup>lt;sup>2</sup> Proc. Bost. Soc. Nat. Hist., XVII. p. 230, 1874.

<sup>3</sup> See description of Oxyn. oxynotum.

<sup>&</sup>lt;sup>4</sup> If, as supposed by Quenstedt, a hollow keel also existed in Agassiceras, this argument is much strengthened, since this genus is in our view more decidedly arietian in its characteristics than Oxynoticeras.

stouter varieties of oxynotum. On the other hand, the duration of the striaries-like stage in Greenoughi, the sutures of the adult, which are simpler or more arietian in outline than in oxynotum, and the essentially hollow keel, seem to indicate an independent origin directly from Agas. striaries. The specimen of Greenoughi in the Museum of Stuttgardt, in which the hollow keel was observed, had the outer shell of the keel remarkably thick, but the interior evidently hollow, while in the French specimens at Semur the shell of the keel was of usual thickness. The former may possibly indicate a transition to oxynotum.

Oxyn. Guibali, however, by the resemblances of the young to the adult of Greenoughi, and by the younger period at which the adult characteristics of the species are inherited, is apparently a direct derivative from Greenoughi. The same reasons would also apply to Lotharingum, in which the young lose the striaries-like stage almost entirely, and repeat only the adult form and characteristics of Greenoughi. These characteristics, the continual decrease in the duration of the adult stages, and the earlier period at which the senile stage of decline makes its appearance in each successive species, indicate that these three species belong to a distinct subseries from oxynotum. The earliest representatives are found in the Tuberculatus bed at Semur, and in the Oxynotus bed of Dumortier in the basin of the Rhone. The different species seem, therefore, to form two subseries; one consisting of oxynotum and its allies, and another composed of Greenoughi, with Guibali and Lotharingum and their allies, but all on the same geological horizons.

#### FIRST SUBSERIES.

## Oxynoticeras oxynotum, HYATT.

Plate X. Fig. 4, 5, 14-22, 27. Summ. Pl. XIII. Fig. 9, 10.

Amm. oxynotus, Quenst., Petrefactkunde, XCVIII., pl. v. fig. 11; Amm. Schwäb. Jura, pl. xxii. fig. 28-49. Amaltheus oxynotus, Wright, Lias Amm., pl. xlvi. fig. 4-6. Amm. oxynotus, Dum., Étud. Pal. Bassin du Rhone, pl. xxxiii. fig. 2, 3, 5 (not fig. 1, 4).

Localities. — Lyme Regis, Cheltenham, Stonehouse, Gloucester, Hanover, Pliensbach, Balingen, Salins.

The young are at first smooth, and in this early stage resemble closely Psiloceras. They may continue to retain this smoothness and the rotundity of the abdomen until the specimen is 12 mm. in diameter, as figured on Plate X. Fig. 17. Their sides then become flatter, and slight folds and striations appear. The resemblance to Agas. striaries is so decided in some young specimens, that, if found independently, no one would hesitate to place them in the same genus as closely allied species. This same resemblance also necessarily includes a close likeness in the young to Psil. planorbe. The sutures are also similar to those of Agas. striaries, as may be seen in collections at Stuttgardt, where there is a very fine series of exceptional varieties collected by Professor Fraas.

The keel appears much later in the *striaries*-like forms figured on Plate X. Fig. 4, 5, than in the normal forms figured on Plate X. Fig. 16–18, but in all varieties the arietian characteristics of the sutures are apparent. The keel on its first appearance seems to be solid, though I could not, as in the case of

Oxyn. Lotharingum, determine this with absolute precision. If this could have been unquestionably settled, the evidence of descent from striaries would have acquired additional probability.

There is also an interesting variety which resembles the young of Amalheus margarilatus, having even the crenulated abdomen, as figured on Plate X. Fig. 19. This leads into a variety having a blunter and deeply crenulated abdomen, as in Phylloceras Bobluyi, and also resembling it in form, though distinct in the sutures (Plate X. Fig. 20). The involution, however, is irregular, decreasing with age, instead of preserving the normal amount of increase, though the specimens did not exceed an inch in diameter. These and Quenstedt's observation and figures, especially in his "Ammoniten des Schwäbischen Jura," show that all crenulated specimens in this group are probably pathological, and also in most cases dwarfish.

The typical form, figured on Plate X. Fig. 18, prevails in the majority of specimens, and the resemblance of these to the young of *striaries* is very much obscured by the early development of the compressed adult form, the sharp keel, and characteristic sutures of the species.

The structure of the keel in one specimen at Semur was plainly visible (Plate X. Fig. 27). The external shell enveloped the cavity of the keel and the internal nacreous layer formed a convex floor, but the space between these two, instead of being hollow as in Oxyn. Greenoughi, was filled by layers of shell. These were thickest at the centre and gradually diminished to either side. Their attenuated lateral extensions formed a third layer between the outer shell and the nacreous lining, but how far this extended upon the sides was not ascertained. The dark-colored layer, which was considered an essential characteristic of a fully developed hollow keel by Baron Schwartz, is also present, lying just above the nacreous lining and a little on one side.

Besides these forms, there is at Semur, identified as a form of Lotharingus by Reynés, a variety of this species which attains the large size of 393 mm. Even at this size the characteristic form of the adult is maintained, though the involution is perceptibly less, the umbilicus being quite open. Oxyn. oxynotum is the only species of the group which attains as large size in its normal variety without losing the keel, and therefore I think the specimen belongs to this species. The examination of old and young forms at Semur enables us to state, that in extreme old age, when the shell is about 335 mm. in diameter, the form sometimes changes. The keel becomes very broad, a depressed zone makes its appearance on the sides near the umbilicus, and the involution becomes so much less that I have compared the aspect of the umbilicus to that of Amm. Romani.

The examination of specimens of *oxynotum* in the École des Mines at Paris showed a very thin external layer of shell near the abdomen, a thicker internal

¹ The small specimens figured by Canavari on Plate VI. of the work so often quoted above, as Amaltheus margaritatus and actaonoides, and Ariet. (Oxynoticeras) Castagnolai, are probably all related to these peculiar pathological forms, and are, notwithstanding their close imitation of the characteristics of Amaltheus, really only morphological equivalents. Canavari has himself referred Castagnolai to Oxynoticeras, and this is evidently an entirely distinct species from that figured by Wähner as Castagnolai, which in our opinion is a species of Caloceras.

layer, which formed the partition above the keel, and above this again a succession of finer layers; but these did not fill up the interior of the keel completely. A hollow portion or zone filled in the fossil with pyrites, occupied the outer half of the interior of the keel. My notes and sketches make no mention of any dark layer in these specimens.

## Oxynoticeras Simpsoni, HYATT.

Summ. Pl. XIII. Fig. 11.

Amm. Simpsoni, Simps., Amm. York. Lias, p. 37.

Amaltheus Simpsoni, Wright, Lias Amm., p. 392, pl. xlvii. fig. 4-7.

Amm. oxynotus (pars), Dum., Étud. Pal. Bassin du Rhone, pl. xxxiii. fig. 1, 4? (not fig. 2, 3, 5).

Locality. — Whitby.

This species is quite different in form, sutures, and the amount of involution, and it is better to hold it as distinct than to confuse it with oxynotum.

It is admirably figured by Wright. The shell is considerably more tumid, the whorl thicker and stouter than in oxynolum, and this peculiarity is observable even in the young. The amount of involution is greater, and consequently the umbilicus is smaller, than in that species. The margins of the sutures are much simpler, especially as regards the auxiliary lobes and saddles than in oxynotum. It is intermediate in all its characteristics between oxynotum and Lymense, and this is an additional reason for separating it from the former.

If we are right, either this species or a form transitional to it is found in the basin of the Rhone.

#### Oxynoticeras Lymense, HYATT.

Summ. Pl. XIII. Fig. 12.

Amaltheus Lymensis, Wright, Lias Amm., pl. xlvi. fig. 1-3; pl. xlvii. fig. 1-3; pl. xlviii. fig. 1, 2. Amm. Sæmanni, Dum., Étud. Pal. Bassin du Rhone, p. 154, pl. xl., xliii. Amm. oxynotus, Hauer, Ceph. Nordöstl. Alpen, pl. xiii. fig. 3, 4, 8, 9 (not fig. 6, 7).

Locality. - Lyme Regis.

This is merely a more involute form of Oxyn. oxynotum, which deserves a separate name on this account, but is closely related to that species.

# Oxynoticeras numismale, HYATT.

Amm. oxynotus numismalis, Quenst., Amm. Schwäb. Jura, p. 289, pl. xxxvii. fig. 1-3, 6, 7 (not fig. 4, 5). Amaltheus Wiltshirei, Wright, Lias Amm., pl. xlviii. fig. 3.

Locality. — Boll.

This species has, according to Quenstedt's figures, young similar to the adults of oxynotum, and the adult has a hollow keel. This is lost in old age, the whorl becoming rounded as in Lotharingum. It seems to be an extremely geratologous form of the first subseries surviving in the Middle Lias. The sutures are oxynoticeran in outline, and confirm this view of the affinities of the species.

Quenstedt considers it identical with Oxyn. Oppeli, which is, however, a stouter form at the same stages of growth. He also erroneously identifies it with Oxyn.

Lymense as described by Wright. The senile stages separate it from the last, though it is probably closely allied, and might be considered a variety if occurring in the same bed. Wright's Willshirei, which seems to be identical, was found in the Henleyi bed of the Middle Lias.

## SECOND SUBSERIES.

# Oxynoticeras Greenoughi, HYATT.

Plate X. Fig. 30. Summ. Pl. XIII. Fig. 13.

Amm. Greenoughi, Sow., Min. Conch., II. p. 71, pl. exxxii. Amm. Greenoughi, HAUER, Ceph. Nordöstl. Alpen, p. 46, pl. xii. Amm. oxynotus, HAUER, Ibid., pl. xiii. fig. 6, 7 (not fig. 3, 4, 8, 9). Amaltheus Greenoughi, WRIGHT, Lias Ammonites, p. 384, pl. xliv. Amaltheus Guibalianus, WRIGHT, Ibid., p. 385, pl. xlv. Amm. Guilbalianus, D'Orb., Terr. Jurass. Ceph., p. 259, pl. lxxiii. Amm. Guibalianus, REYNÉS, Plates (pars).

Amm. Guibali, REYNÉS, Ibid.

The examination of German specimens led to the conclusion that this species was closely allied to oxynotum in development and in sutures, and the splendid suite of this species at Semur enabled us to solve all difficulties.

Here also we were able to compare it with specimens of the true Collenoti, D'Orb., the originals of which are in the Museum of Comparative Zoölogy, and they have not the slightest claim to be considered identical. Oppel was probably led astray by what he supposed to be the types in D'Orbigny's collection.

Reynés has divided this species into three forms, not very readily distinguishable by their adult characteristics, but quite distinct when their development and old age are studied. His principal observations on Lotharingus, Guibali, and Greenoughi were made in the Museum at Semur. We however refer his Guibali to Greenoughi, because of their close resemblance in development and old age, and, in order to avoid the use of a new name, distinguish the next species, his Guibalianus, as Guibali. This also is justified by the types in the Semur collection, in several of which these names are interchanged. The true Guibalianus, D'Orb., as may be seen by comparison of the original specimen and the Semur collection, has more abrupt umbilical shoulders, a more open umbilicus, less involute whorls, and retains the keel and typical form of the whorls until a later stage of growth than any of the group except oxynotum.

The shell sometimes attains the size of 235 mm. before any marked change of form is observable, and in one specimen reached the size of 410 mm. before the keel disappeared. Finally, however, the keel begins to disappear, and eventually all traces of it vanish in the rounded abdomen. The form, however, seldom changes as completely as in Guibali. The length of the ribs, whether they are all long or alternately long and short, is a characteristic of great variability, and is of no use in distinguishing the species.

There are, so far as we have seen, no representatives of this subseries in the South German basin, and this observation is sustained by Quenstedt's "Ammoniten des Schwäbischen Jura," which does not contain a single undoubted form

of this subseries. Quenstedt's Amm. Guibalianus is not a true Greenoughi, and is properly referred by him to the radians group. An error is also shown by the use of this name for a species of the Middle Lias, since Guibalianus does not occur above the Lower Lias.

The species as figured by Wright is a large shell, about 475 mm. in diameter, which has already lost the keel and pilæ, the abdomen being rounded. The internal whorls of the original are heavily pilated, but the last whorl and a half are smooth. Sowerby's figure is taken from a very large and aged specimen, and the pilations shown in the umbilicus indicate a shell with heavier folds at the same age than exist in either Hauer's or Wright's figures. Wright's descriptions, however, coincide with Sowerby's figure, and the old of Sowerby's shell has a completely elliptical aged whorl. The size at which senility affects the shells, and the general characters and aspect of these figures, are the same as in *Greenoughi*. The young forms figured by Hauer may possibly be the young of this species; they seem to be too heavily pilated for the young of oxynotum.

# Oxynoticeras Guibali, HYATT.

Pl. X. Fig. 28, 29, 31. Summ. Pl. XIII. Fig. 14,

Amm. victoris, Dum., Études Pal. Bass. du Rhone, II. p. 136, pl. xxxi., xlii. Amm. Guibali, Reynés, Plates (pars). Amm. Guibalianus, Reynés, Ibid.

Locality. - Lyme Regis?

The keel of this species may begin to disappear in some specimens even at the size of 100 mm. In one specimen of the Semur collection this is accompanied by a singular and marked lateral deflection of the hollow keel, and at the size of 170 to 180 mm. it had wholly disappeared, and the outer whorl had a very broad and gibbous abdomen; the sides, however, remained convergent and rounded.

There is a specimen of this species from Lyme Regis in the Museum of Comparative Zoölogy, which was found associated in the same slab with Cal. carusense and raricostatum. The diameter of this specimen is 145 mm. The keel is not present on the cast, as is usual in this species, but it had probably been present in the perfect shell, and evidently not impaired by age; the whorl and involution of the sides were also not altered from the adult condition. A section showing the inner whorls had been formed by fracture, and the outlines of these, the hollow keel, and the amount of involution of the whorls, are the same as in Oxyn. Guibali.

Anm. victoris, Dum., is evidently closely allied to Greenoughi, but, as figured by Dumortier, presents very peculiar sutures. It attains a large size before losing the keel, though one was seen by Dumortier which at a diameter of 456 mm. had no keel. It may prove to be a form which is transitional between Greenoughi and this species.

### Oxynoticeras Buvigneri, HYATT

Amm. Buvigneri, D'Orb., Terr. Jurass. Ceph., pl. lxxiv. Amm. Buvigneri, Dum., Études Pal. Bass. du Rhone, p. 147, pl. xxxiv.

The original is not correctly figured by D'Orbigny. The specimen is altered by compression, and this distortion is represented in his figure as natural; it has one side more compressed than the other, and this side has been selected in his figure as characteristic of both sides. The abdomen of the original also possesses a keel, which is not shown in the figure. The figure is, however, near enough to that given by Dumortier to enable one to identify it as the same, and the fact that it has a keel is an important point in this connection. It is much more involute than any species of the *Greenoughi* subseries except *Lotharingum*, but from this last it can be distinguished by the much larger size attained before the keel is lost. Dumortier's specimen reached the diameter of 126 mm., and D'Orbigny's that of 184 mm., without perceptible marks of senile degeneration. We regard this difference as an uncertain characteristic, but have no means of verifying the connection with *Lotharingum*.

## Oxynoticeras Lotharingum, HYATT.

Plate X. Fig. 23-26. Summ. Pl. XIII. Fig. 15.

Amm. Lotharingus, REYNÉS, Plates.

In this species at the size of 100 mm, the keel had almost disappeared, and the pilæ in several instances crossed the abdomen. The abdomen had become rounded, but the involution had not perceptibly decreased. The umbilicus is smaller in the adult, the whorls stouter in proportion than in the preceding species, and the characteristic form and aspect of *Greenoughi* are found only in the young. The younger stages had a solid keel, the hollow keel occurring only at later stages of growth and in adults, and it suffered from degeneration and finally disappeared in the senile stage. This is one of the most interesting examples yet discovered of the similarities of the old and young stages in the same individual. The resemblances which usually exist between the old and young shell are also present, and the absence of the hollow keel in extreme old age shows how seriously the organization may degenerate after the adult period, even with regard to the most important structural differentiations.

#### Oxynoticeras Aballoense, HYATT.

Amm. Aballoense, Dum., Études Pal. Bass. du Rhone, p. 141, pl. xxvii. fig. 1,2; pl. xxviii. fig. 1; pl. xxxviii. fig. 1-3; pl. xl. fig. 1.

This species as described and figured by Dumortier seems to be quite different from *Greenoughi*, and yet the stouter specimens of that species certainly approximate to it quite closely. We have not the means at hand of finding by comparison whether the principal characteristics cited by Dumortier, namely, the deep umbilicus and abrupt shoulders of the whorls on the edge of the umbilici,

are present also in *Greenoughi*, and therefore retain the separate appellation given by him. There is also a possible relationship with the *Oxyn. Oppeli* of the Middle Lias, which makes it desirable to keep it separate, for the present at least, from *Guibalianum*. If it is a distinct species, or even a distinct variety, of *Greenoughi*, it may be the immediate ancestor of *Oppeli*.

### Oxynoticeras Oppeli, Schlön.

Summ. Pl. XIII. Fig. 16.

Oxynoticeras Oppeli, Schlön., Zeit. deutsch. Gesells., XV. p. 515.

Amm. Oppeli, Schlön., Paleontogr., XIII. p. 161, pl. xxvi. fig. 4, 5.

Amm. Oppeli, Dum., Études Pal. Bass. du Rhone, p. 125, pl. xxxv., xxxvi.

Amm. oxynotus numismalis, Quenst., Amm. Schwäb. Jura, p. 298, pl. xxxvii., fig. 4, 5 (not fig. 1-3, 6, 7).

The peculiar stout form of this species at the same age distinguishes it readily from the Middle Lias congener of the same name described and figured by Quenstedt. The stout form of the young, gibbous sides, and the blunted abdomen, show that it may have been a member of a subseries in which Aballoense was the first representative in the Lower Lias. The figure by Dumortier exhibits a prominent keel even at the diameter of 165 mm. Schlönbach's specimens did not completely lose the keel until over 500 mm. in diameter.

Geyer in his Liass. Ceph. Hierlatz b. Hallstadt gives Oxyn. oxynotum, Guibalianum, and a form allied to the latter under the name of Oxyn. cf. Collenoti; also two undetermined species and a distorted form, named Oxyn. Janus. These are all small and dwarfish, except the first, which, however, cannot be called large, the largest individual measured by Geyer having been found to be only 74 mm. in diameter.

<sup>&</sup>lt;sup>1</sup> Amm. Schwäb. Jura, pl. xxxvii. fig. 1-3, 6, 7.



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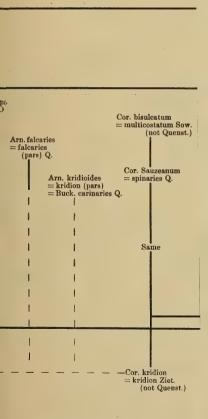
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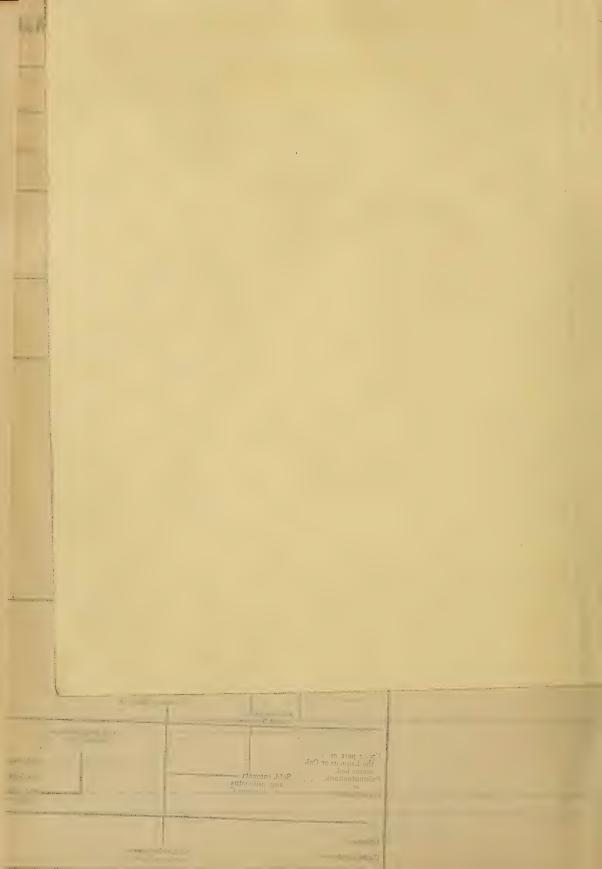
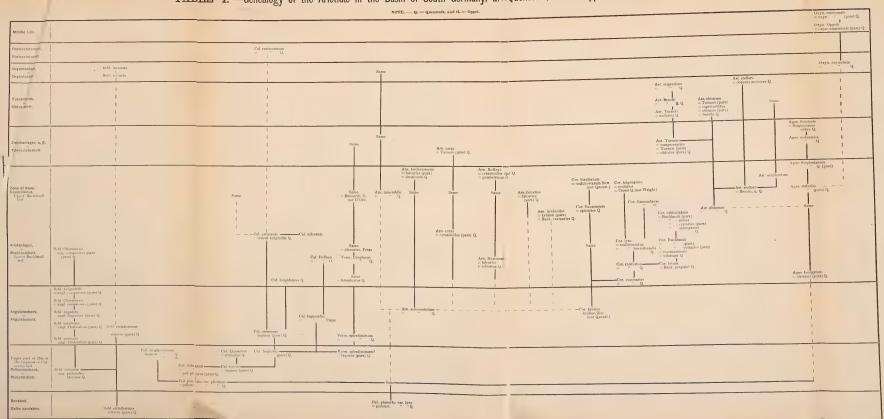
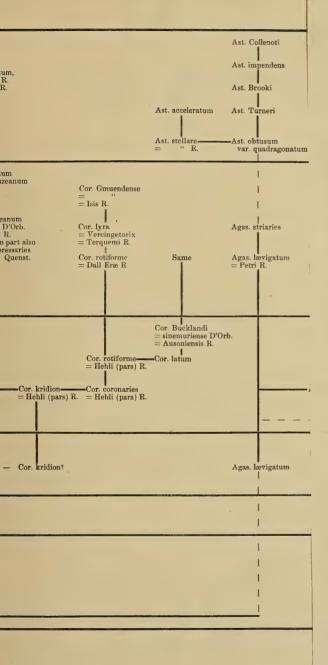


TABLE I. — Genealogy of the Arietidæ in the Basin of South Germany, afteQuenstedt, Fraas, Oppel, and their Collections.



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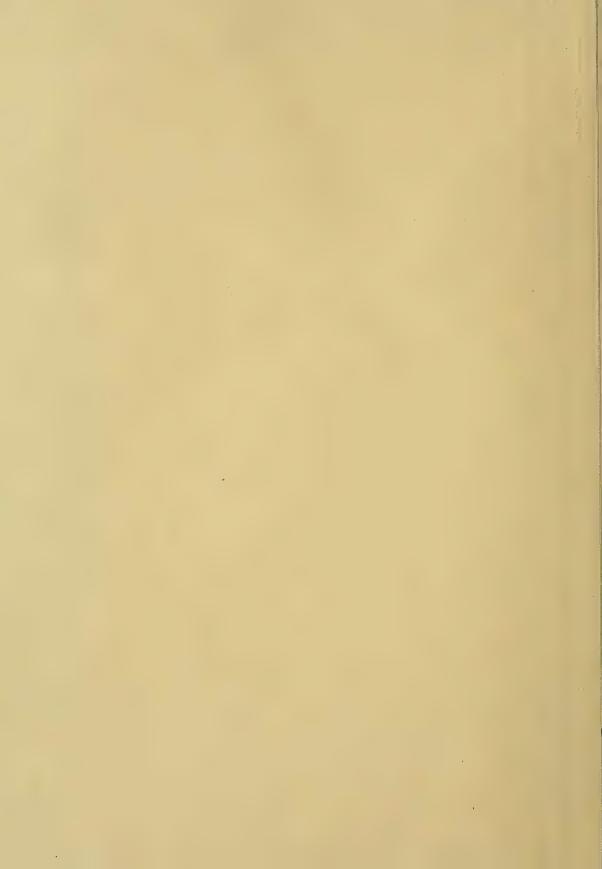
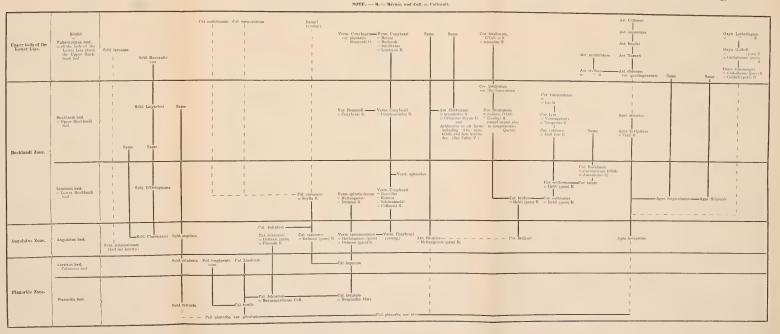
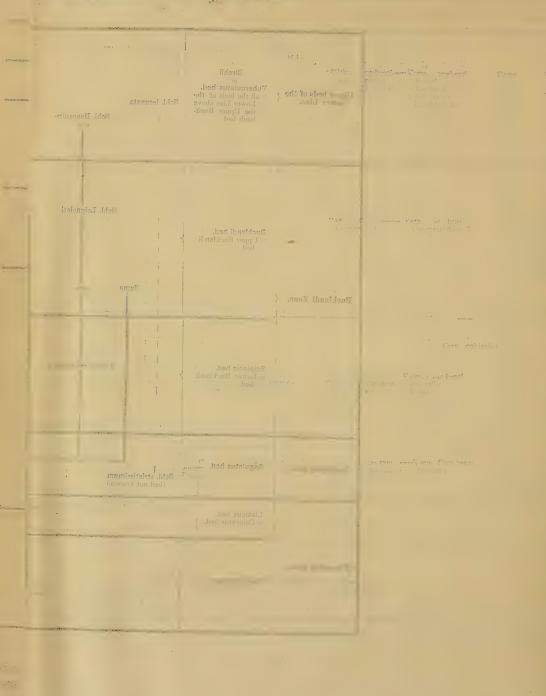


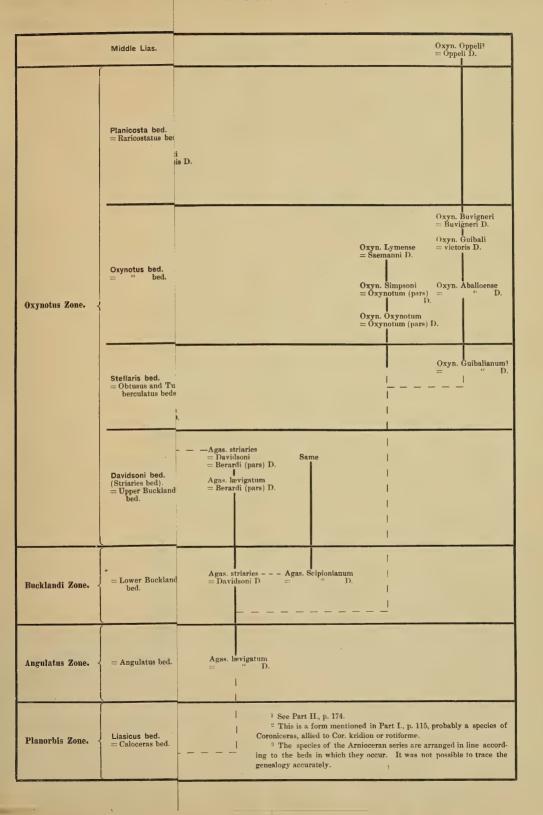
TABLE II. — Genealogy of the Arietidæ in the Basin of the Côte d'Or, after Collenot and the Collections at Semur, and Boucault's Collection in Museum of Comparative Zoölogy.



# TABLE II - (couly) of the



## Dumortier.



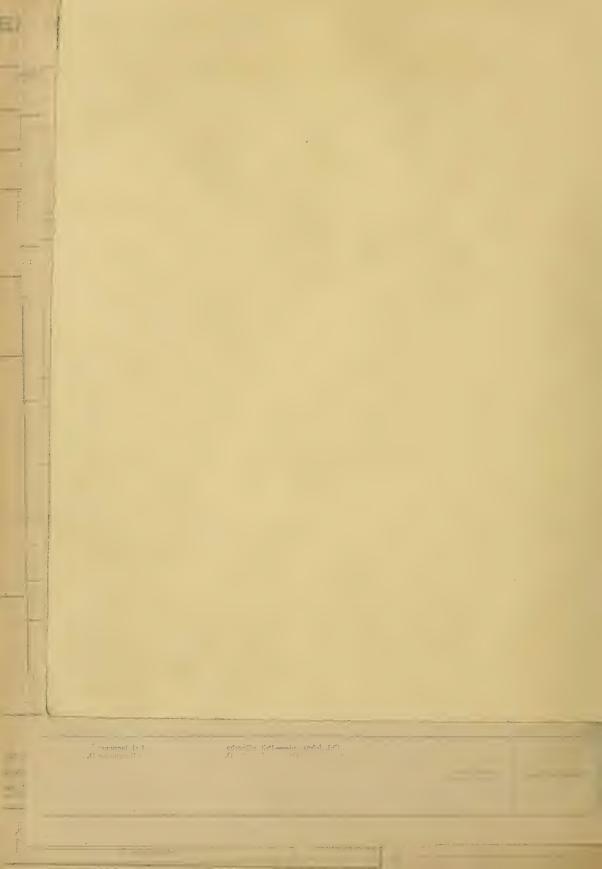
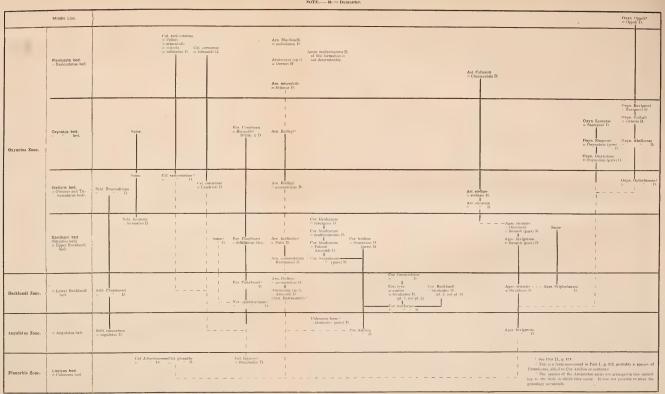


TABLE III. - Genealogy of the Arietidæ in the Basin of the Rhone, after Dumortier.

NOTE. --- D. == Dumortler.



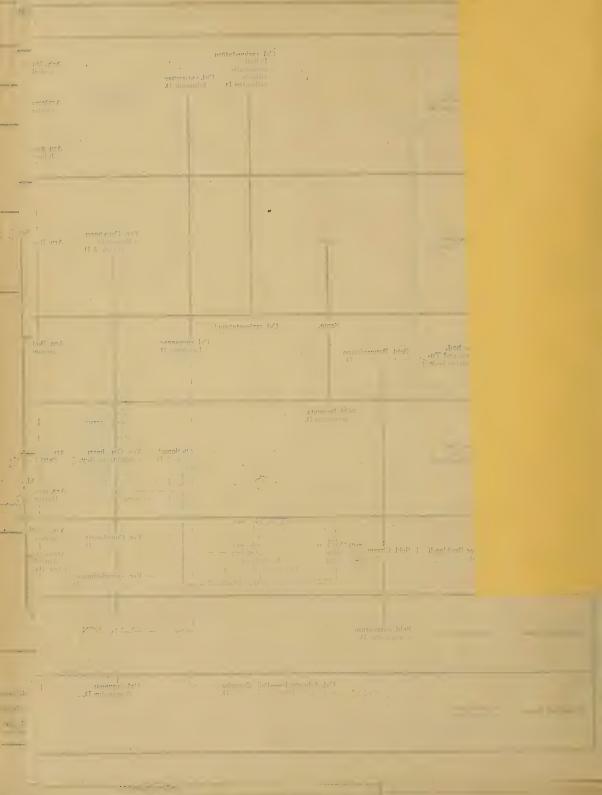
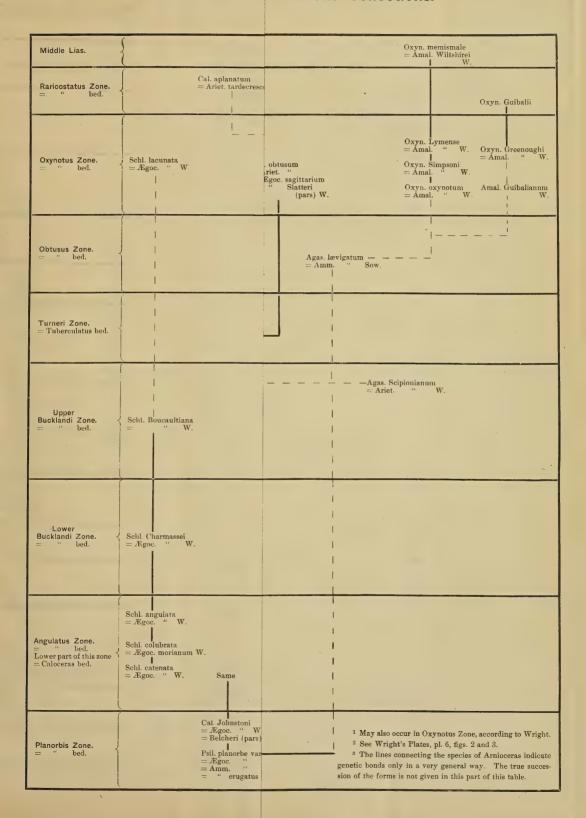
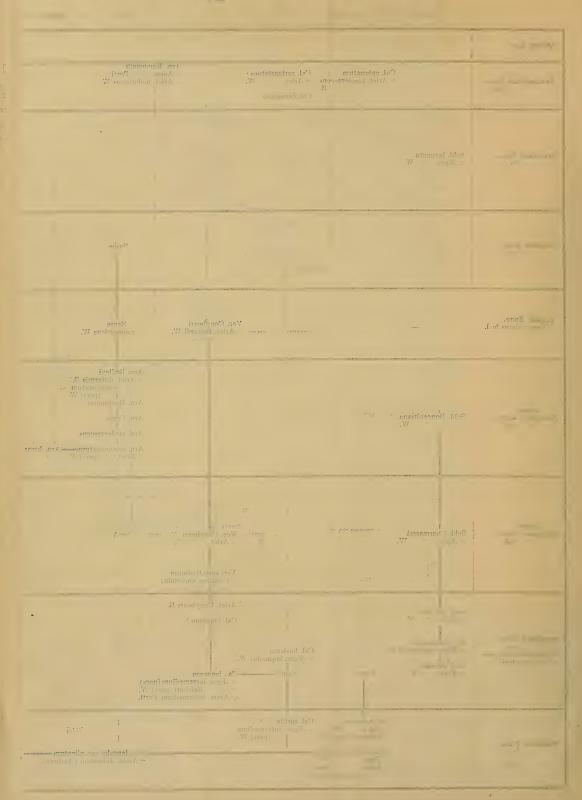


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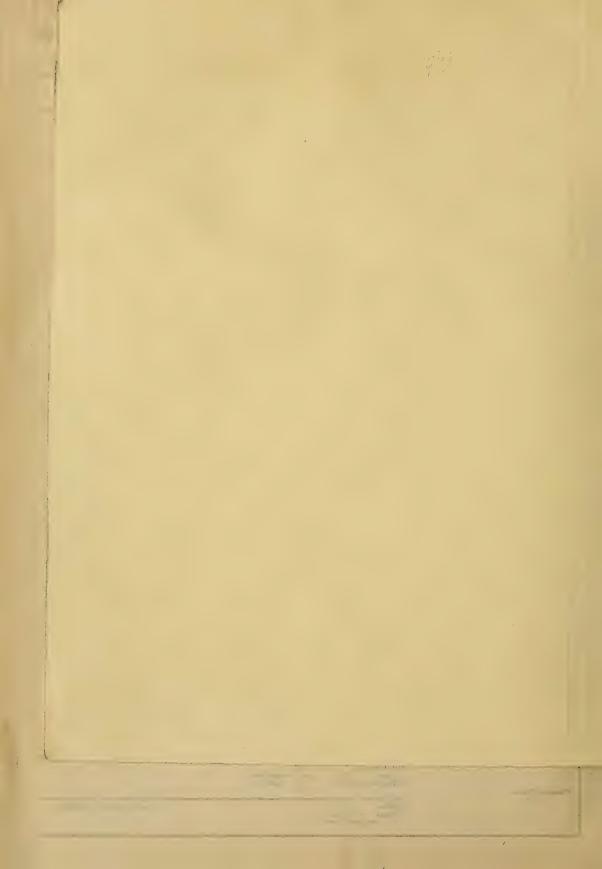
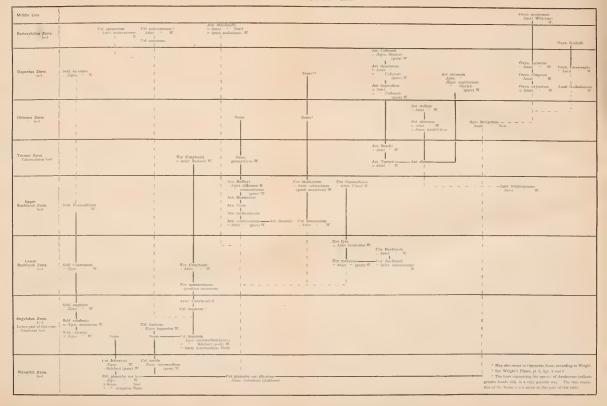
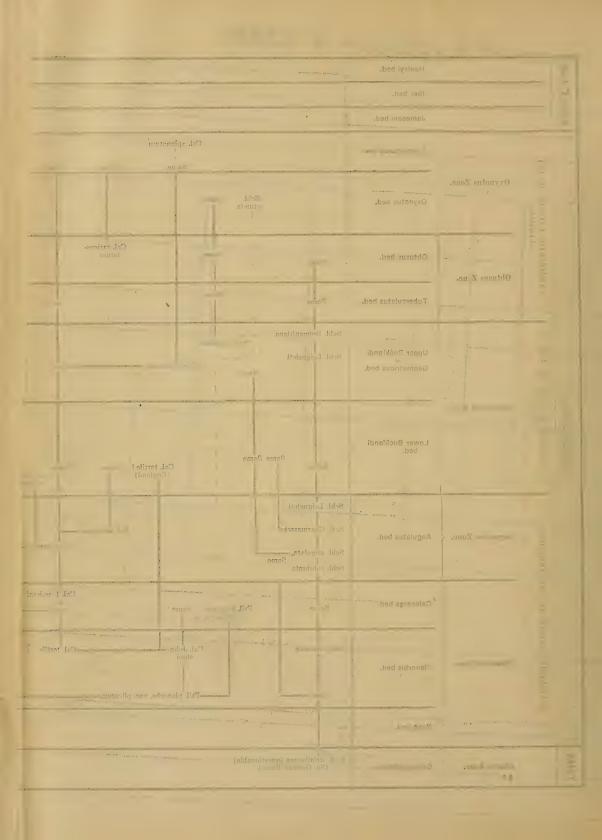


TABLE IV. — Genealogy of the Arietidæ in the Basin of England, after Wright and various Collections.

NOTE. - W. = Wright, and B. = Blake.

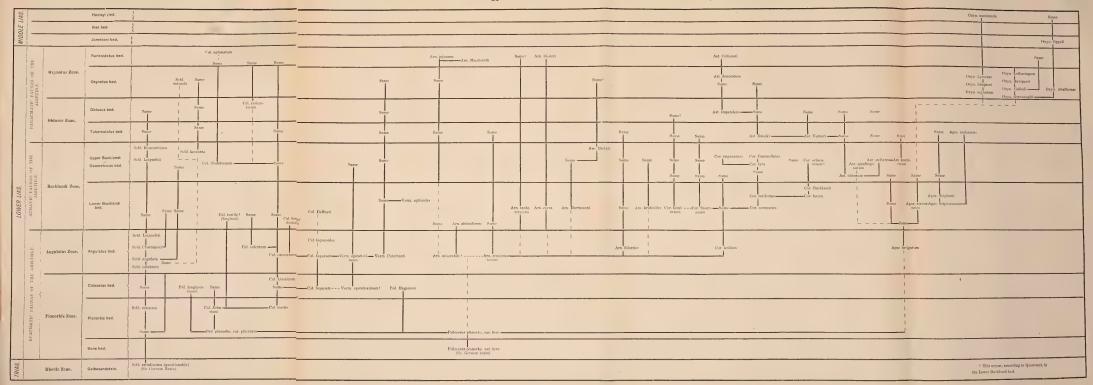




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TABLE V. — Genealogy of the Arietidæ in the Province of Central Europe.



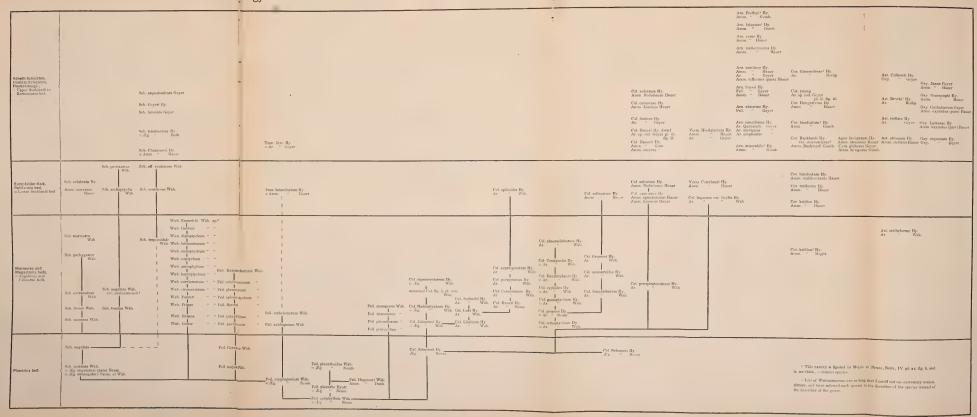
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#### EXPLANATION OF PLATES.

ALL specimens not otherwise described are in the collection of the Museum of Comparative Zoölogy, and all not mentioned as "casts" have the shell present, either in part or as a whole. Paul Roetter drew the figures in outline by measurement; the author redrew all the specimens using these outlines, but testing the accuracy of the measurements before they were finally placed on stone. The outlines in the Summary Plates were sketched by the author, and redrawn by Miss Pierson. Unless otherwise specified, the figures are approximately of natural size, although the process of reducing by photography from the enlarged drawings has introduced some slight deviations from the measured diameters of the originals.



TABLE VI. — Generalogy of the Arietidæ in the Mediterranean Province, after Hauer, Neumayr, Wähner, Mojsisovics, Herbich, Gümbel, Geyer, and Rothpletz.



## PLATE I.

Psil. planorbe. Fig. 1, cast with incomplete living chamber, showing folds at an early stage of growth. Fig. 2, suture much enlarged. Loc. Whitby. Fig. 3, 4, cast with similar folds in the young, but smooth in the adult. Fig. 4a, young of Fig. 4 enlarged. Loc. Neuffen. Fig. 5, 6, cast of the more involute variety, loc. Balingen. The specimen has distorted sutures, showing the broad abdominal lobe and the large median saddle on one side, but is otherwise normally formed.

Cal. Nodotianum. Fig. 7,¹ specimen reduced to less than one half, showing incomplete living chamber. Fig. 8, sutures enlarged. Fig. 9, a fragment of a cast showing sutures and part of living chamber. Fig. 10, section of four whorls. Fig. 11, a cast. Fig. 11 a, section of last whorl. Loc. Semur.

Cal. tortile. Fig. 12, specimen with portion of living chamber. Fig. 13, same, portions of the two outer whorls removed, showing their rounder outlines. Fig. 14, suture of same, enlarged. Loc. Semur.

Cal. carusense.<sup>2</sup> Fig. 15, cast of the younger stages, broken out of the interior of an adult specimen, loc. Balingen. Fig. 16, cast, loc. St. Thibault.

Verm. spiratissimum. Fig. 17, cast, living chamber incomplete, loc. Nellingen. Fig. 18, specimen with distinct channels, developed at an early age, loc. Semur.

Cal. sulcatum. Fig. 19, specimen with incomplete living chamber, showing the smooth young in the centre. Fig. 20, suture of the same, enlarged. Loc. Semur.

Verm. ophioides. Fig. 21, cast of a broken specimen, showing the well developed channels and keel in the young, and the early appearance of the pile. Figs. 22, 23, sutures of this and an older specimen, enlarged. Loc. Semur.

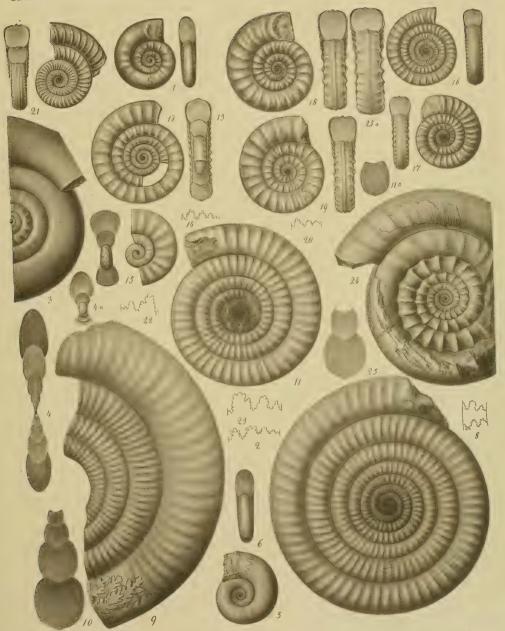
Cal. raricostatum. Fig. 24, specimen, showing the senile metamorphoses. Fig. 25, section of last two whorls, showing the corresponding change of form for comparison with Fig. 25 a, the adult of the same variety. Loc. Balingen.

<sup>1</sup> This figure is not numbered.

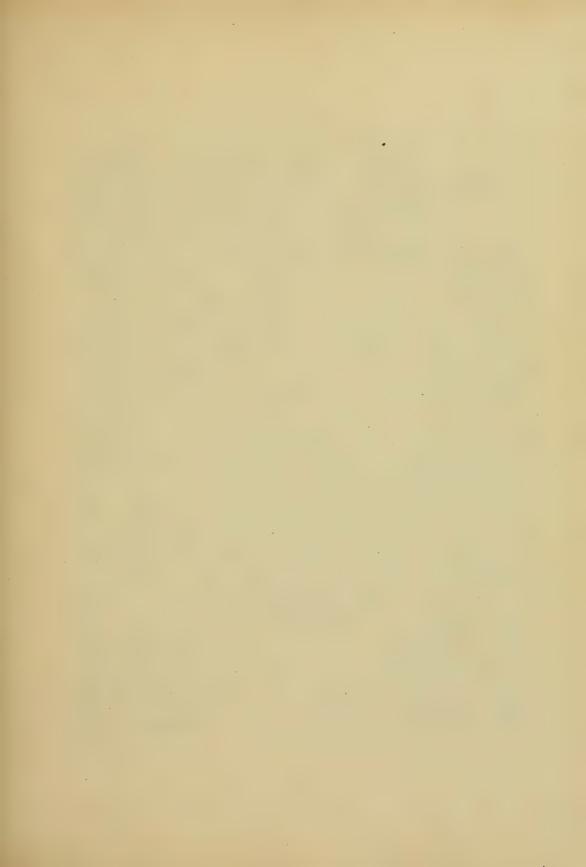
<sup>2</sup> See Plate II. Fig. 1.

See Plate VI. Fig. 15, for the Johnstoni-like variety.

GENESIS OF THE ARIETIDAE.







### PLATE II.

Cal. carusense. Fig. 1, specimen reduced to one third, showing incomplete living chamber and old age. Fig. 2, the same broken so as to show sections of the old whorls and the depressed abdomen of the adult stage. Fig. 3, enlarged adult sutures, also shown on Fig. 1. Fig. 3 a, same, but very old, also shown on Fig. 1. Loc. Semur.

Arn. miserabile. Fig. 4, large smooth specimen, with sutures and incomplete living chamber. Fig. 5, cast with sharp abdomen and gibbous sides, living chamber incomplete. Fig. 6, enlarged sutures of the same. Fig. 7, var. cuneiforme, with incomplete living chamber. Loc. Semur.

Arn. obtusiforme. Fig. 8, section of a cast, showing form of internal whorls. Fig. 9, specimen with incomplete living chamber. Fig. 9 a, enlarged sutures of fig. 9. Loc. Semur.

Arn. semicostatum. Fig. 10, variety with incomplete living chamber, the young remaining smooth until a late period of growth and ribs immature, loc. Semur. Fig. 11, cast, with ribs earlier developed than in Fig. 10, and slightly more prominent. Fig. 12, young from same blocks of limestone. Fig. 13 a, sutures from other young specimens on the same block, of different ages, all natural size. Loc. Whitby. Fig. 14, cast with folds in the extreme young stage and true pilæ beginning afterwards; otherwise the form is perfectly normal, loc. Basle. Fig. 15, normal variety with deep channels. Fig. 15a, suture of the same, enlarged. Fig. 16, specimen with incomplete living chamber, channels developed at an earlier age than in normal variety, and abdomen broader and flatter in proportion than is usual in the species at any age. Loc. Semur.

Arn. Hartmanni.<sup>2</sup> Fig. 17, cast, loc. Bonnert. Fig. 18, suture of the same, enlarged.
 Arn. tardecrescens. Fig. 19, cast of a young specimen with incomplete living chamber.
 Fig. 19 a, enlarged suture. Loc. Yorkshire.

Arn. ceras. Fig. 20 and 20 a, specimen with incomplete living chamber, a very broad abdomen, and deep channels, loc. Semur.

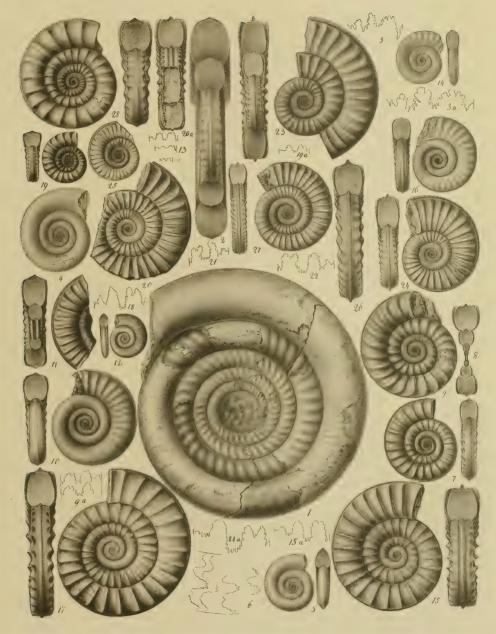
Arn. tardecrescens. Fig. 21 and 22, sutures of a specimen of a normal form (abdomen narrower than the last), at the diameters of 63 mm. and 83 mm. Loc. Semur.

Arn. Bodleyi. Fig. 23, broken specimen, showing planorbis-like folds on the young shell, with living chamber incomplete. Fig. 24, more involute variety with similar fold in the young and incomplete living chamber. Fig. 24 a, suture of the same, enlarged. Loc. Semur.

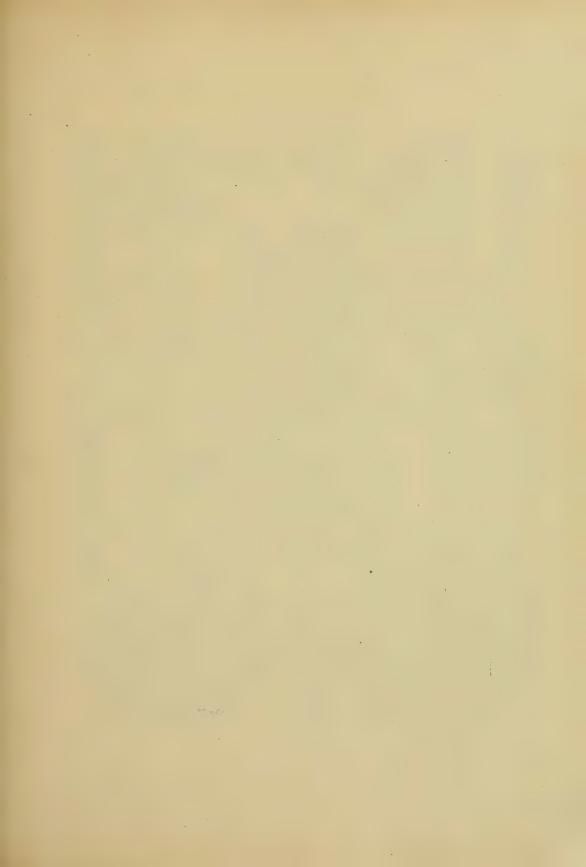
Arn. falcaries. Fig. 25, young with slight tubercles on the geniculæ. The last quarter is part of the living chamber. Fig. 26, larger specimen, ribs not tuberculated or arising from tubercles as in the above, and keel very prominent. Fig. 27, cast with deep channels and abdomen very narrow. Loc. Semur.

Arn. kridioides. Fig. 28, specimen showing the smooth young, the early period at which the pilæ begin, and the similarity of the umbilicus to that of a normal species of Arnioceras. Loc. Basle.

GENESIS OF THE ARIETIDAE.







### PLATE III.

Arn. Hartmanni. Fig. 1, 1 a, cast. Fig. 1 shows the thick shell lying on the keel of the cast. Loc. Lyme Regis.

Cor. kridion. Fig. 2, young. Fig. 2 a, outline of young suture of Fig. 2, enlarged. Fig. 3, cast. The last volution in this represents the living chamber. Loc. Balingen.

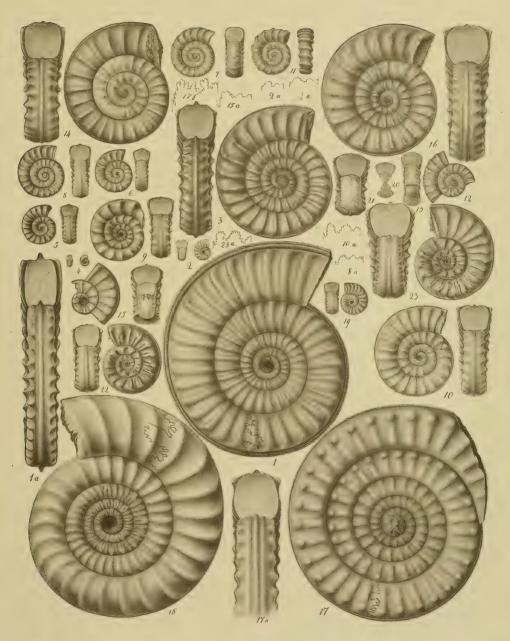
Cor. rotiforme, var. A. Fig. 4-4a, young smooth stage and suture. Fig. 5, 6, 8, 8a-10, 10a, older stages of same. Fig. 7, 11-13, pathological cases with pilæ crossing the abdomen. Loc. Semur. Fig. 14, 15, 15a, 16, kridion-like variety of this species. (Fig. 14, loc. Stuttgardt; Fig. 15, 16, loc. Balingen.) Fig. 17, 17a, variety with discoidal form and large tubercles, figure reduced to about two thirds, loc. Semur. Fig. 17b, sutures.

Cor. Bucklandi, var. sinemuriense. Fig. 18, figure reduced to less than one half, showing the divided pilæ of the young (sinemuriense stage), and the solid Bucklandian pilæ of the adult, loc. Semur.

Cor. latum. Fig. 19, young with narrow abdomen. Fig. 22, older stages of same variety, showing affinities for *Cor. rotiforme* and *Bucklandi*. Fig. 20, section of young of variety with broader abdomen. Fig. 21, 23, 23 a, older stages and suture of same. Loc. Semur.<sup>2</sup>

<sup>&</sup>lt;sup>1</sup> See Plate II. Fig. 17.

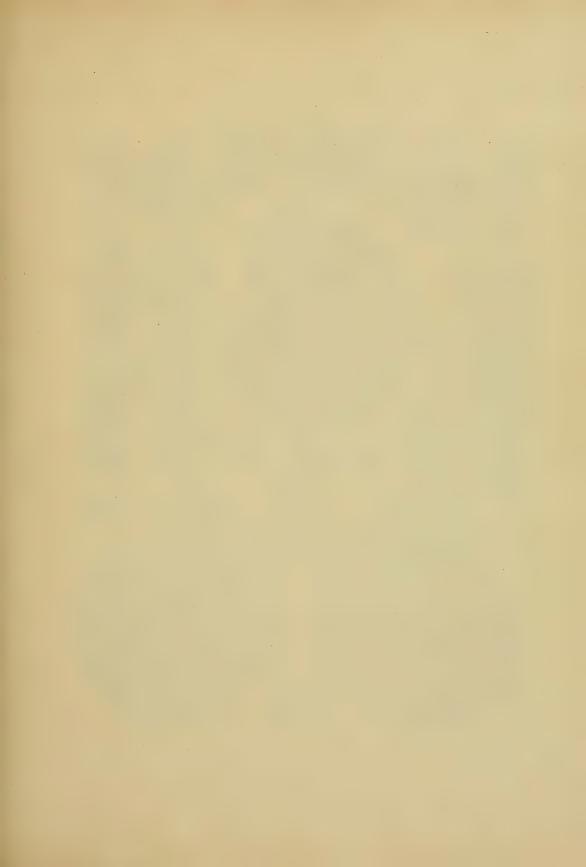
<sup>&</sup>lt;sup>2</sup> These specimens all appear to be in the nealogic stages of development.



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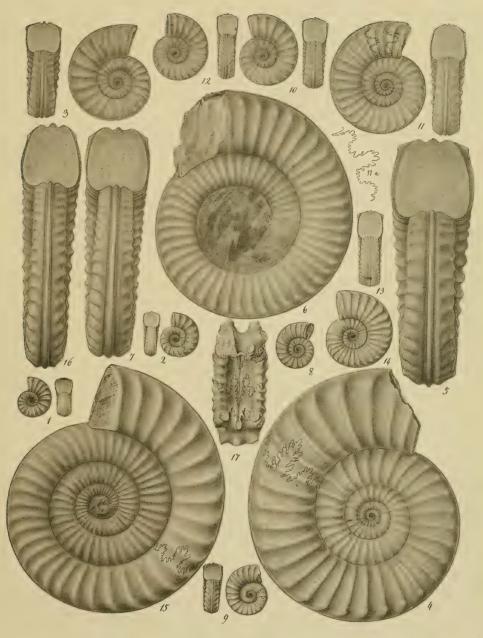


### PLATE IV.

Cor. lyra.<sup>1</sup> Fig. 1, young of variety with broad abdomen and closely arranged pilæ. Fig. 2, young of var. B, with narrower abdomen and rounded sides. Fig. 3, older stage of same variety. Fig. 4, 5, nearly full-grown stage of same variety. Loc. Semur. Fig. 6, 7, full-grown stage of variety with narrower abdomen, flattened sides, and closely arranged pilæ, figure reduced to about one half, loc. Filder. Fig. 8, young of same variety as Fig. 1, but transitional to var. B. Fig. 9-11, young of var. C. Fig. 11 a, suture of same. Fig. 12-14, young of variety like Fig. 1, 1 a, and Fig. 8, but with narrower abdomen and more flattened sides. Loc. Semur. Fig. 15, 16, old specimen of var. C, with very convergent sides, and tubercles considerably reduced, diameter 250 mm., loc. Gmünd. Fig. 17, sutures on the inner side (dorsum), loc. Semur.

<sup>1</sup> See Plate V. Fig. 1-3.

<sup>2</sup> All the specimens figured were casts.







### PLATE V.

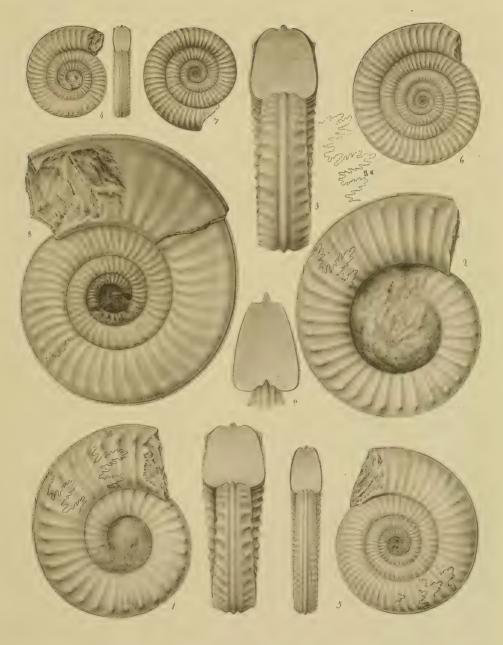
Cor. lyra. Fig. 1-3, half-grown shell of same variety as Fig. 6, 7, Plate IV., showing how narrow the abdomen is in some specimens before the shell was full grown. Fig. 3a, suture, slightly older than that delineated on Fig. 2, showing the changes which had taken place. Loc. Semur.

Cor. Gmuendense.<sup>2</sup> Fig. 4, half-grown specimen, exhibiting variety with discoidal form and compressed whorls, figure reduced to less than one half. Fig. 5, full-grown specimen of same variety with marks of approaching old age upon the last whorl, figure reduced to less than one half. Loc. Semur. Fig. 6, specimen in which the wider abdomen and young proportion of Fig. 4 were maintained until a much later stage than in Fig. 4 or 5, figure reduced to about one half. Fig. 7, umbilicus of Fig. 6, about natural size, to show the smoothness of the young whorls. Loc. Aargau. Fig. 8, 9, same variety as Fig. 5, but showing the effects of senile decline in the convergence of the sides, degeneration of the pilæ and tubercles, diameter 205 mm., loc. Semur.

<sup>1</sup> See Plate IV.

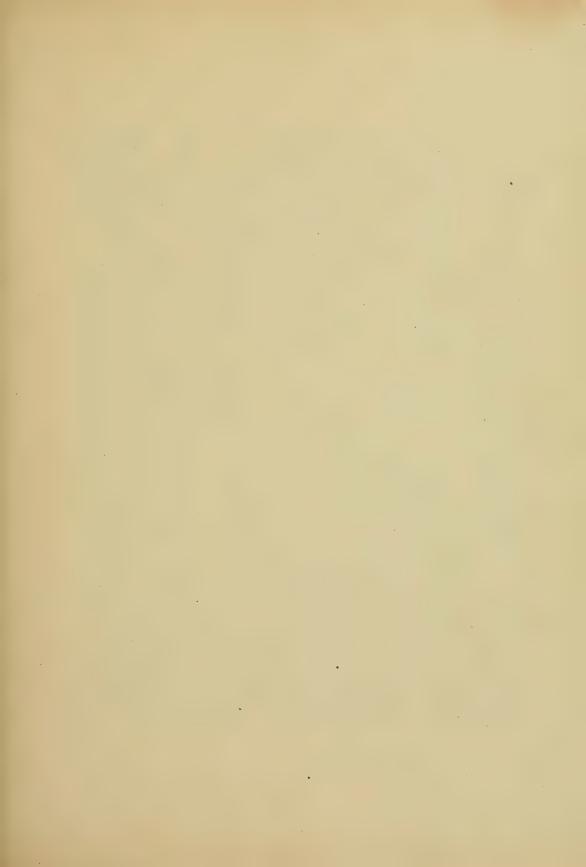
<sup>2</sup> See Plate VI.

GENESIS OF THE ARIETIDAE.



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### PLATE VI.

Cor. Gmuendense. Fig. 1, 2, figures reduced to about one third, taken from a specimen which exhibited compressed whorls and convergent sides at an older stage than in the specimens figured on Plate V. Old age is apparent also in the two closely approximated sutures of outer whorl. Loc. Aalen.

Cor. trigonatum.1 Fig. 3, large variety, having stouter and more numerous whorls, and arriving at the same stage of senile decline later than in the smaller variety described in the text, figure reduced to about one third. Loc. Aalen.

Cor. Sauzeanum.<sup>2</sup> Fig. 4, young, loc. Whitby. Fig. 5, another older specimen, loc. Semur. Fig. 6, another specimen, broken across, showing embryo, and having keel just beginning to be perceptible on the outer whorl. Fig. 7, centre of same section enlarged, showing young whorls. Fig. 8, specimen like Fig. 12, in having no keel on the outer whorl. Fig. 9, variety in which both tubercles and keel appear at an earlier stage. Loc. Whitby. Fig. 10, 11, same variety, showing stouter form of young and earlier developed keel. Fig. 12, 13, D'Orbigny's type, showing the prolonged duration of the smooth stage, and absence of the keel. Fig. 14, adult of var. Gaudryi. Loc. Semur.

Cal. raricostatum.8 Fig. 15, Johnstoni-like variety, loc. Balingen.

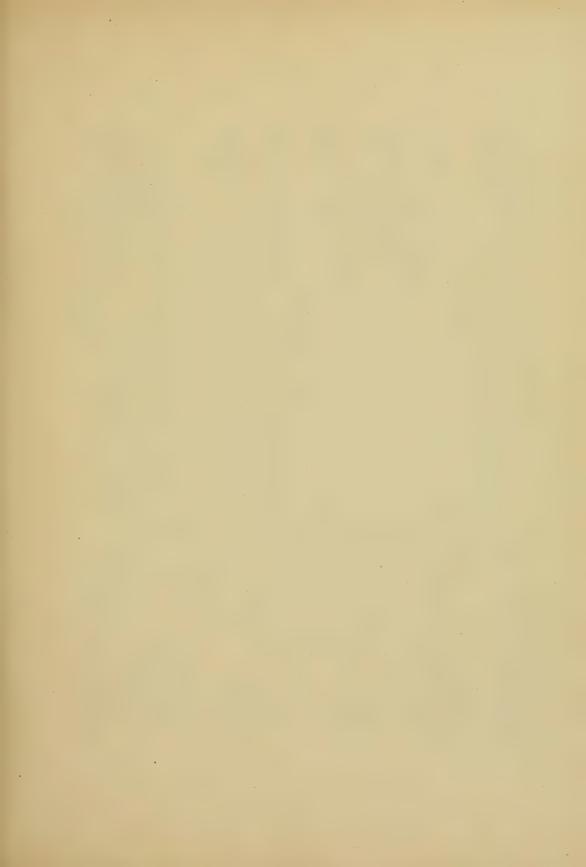
See also Plate VII. Fig. 1, for side view.

<sup>3</sup> See Plate I. Fig. 24, 25.

See Plate VIII. Fig. 1-3.







### PLATE VII.

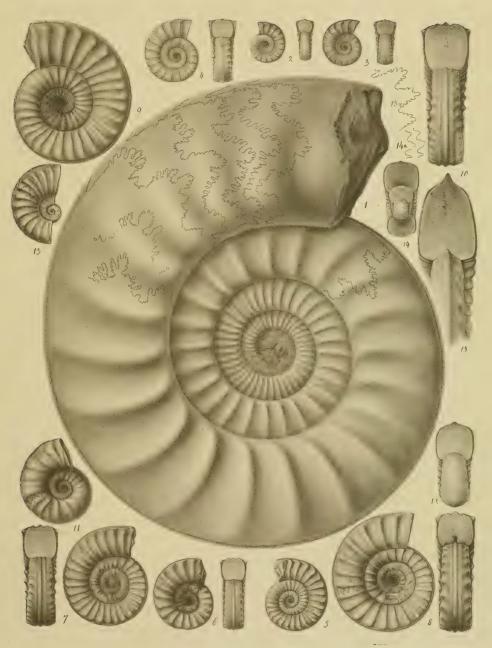
Cor. trigonatum. Fig. 1, old specimen of the stout variety, showing adult suture and the closer approximation and degenerative changes in lobes and saddles in old age, figure reduced to about one third. Loc. Aalen.<sup>1</sup>

Cor. bisulcatum. Fig. 2-4, young. Fig. 5, 6, young with earlier developed and more prominent pilæ. The coarse heavy pilæ of the last figure are remarkable, and the young has also a broader abdomen and a form like an older stage of *Cor. latum*. Fig. 7 shows the decrease in breadth of the abdomen with age, which is also seen in Fig. 6. Fig. 8, older stage, with suture. Fig. 9, 10, nearly full-grown stage of same variety. Loc. Semur.

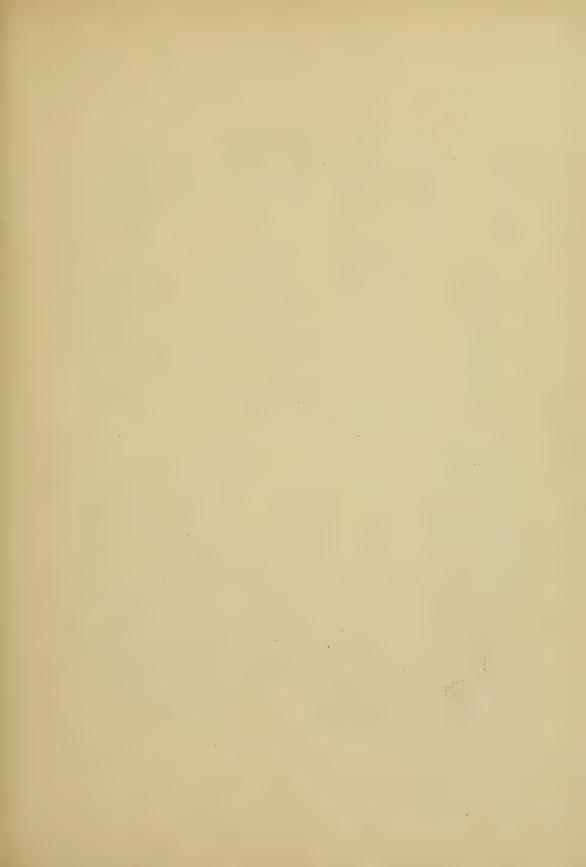
Agas. Scipionianum.<sup>2</sup> Fig. 11, 12, young of gibbous variety. Fig. 13, 14, young, showing development of pilæ from folds. Fig. 13 a, 14 a, enlarged sutures also indicated upon corresponding figures. Fig. 15, front view of same specimen as that of Plate X. Fig. 13. Loc. Semur.

<sup>&</sup>lt;sup>1</sup> See, for ventral view of same, Plate VI. Fig. 3.

<sup>&</sup>lt;sup>2</sup> See Plate X. Fig. 11-13. Summ. Pl. XIII. Fig. 7.







# PLATE VIII.

Cor. Sauzeanum.¹ Fig. 1-3, var. *Gaudryi*, older and younger whorls of the same specimen, loc. Leicestershire. Fig. 3 a, dorsum showing sutures.

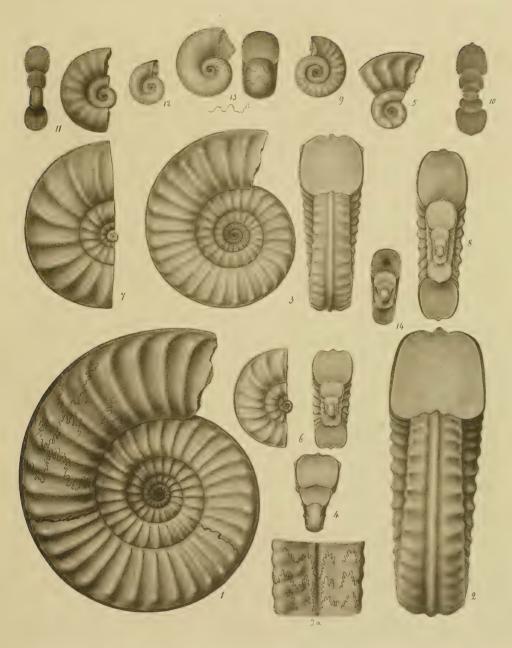
Aster. obtusum.² Fig. 4, 5, young of var. E, showing large tubercles and broad abdo-

men. Fig. 6-8, older stage of same specimen. Loc. Lyme Regis.

Agas. lævigatum. Fig. 9, side view of var. B, with living chamber. Fig. 10, var. D, section showing the extremely broad young and secondary helmet-shape of the later whorls, which are like those of Psiloceras except of course in the keel (the outline of the centre is uncertain except as regards the breadth). Fig. 11, var. A, showing the absence of a keel. Fig. 12, var. D, showing outline of aperture and living chamber, loc. Semur. Fig. 13, very stout young, showing the goniatitic form, and striations like those of Agas. striaries. Fig. 14, section of variety from Lyme Regis.8

<sup>2</sup> See Plate IX. Fig. 1. <sup>1</sup> See Plate VI. Fig. 4-14.

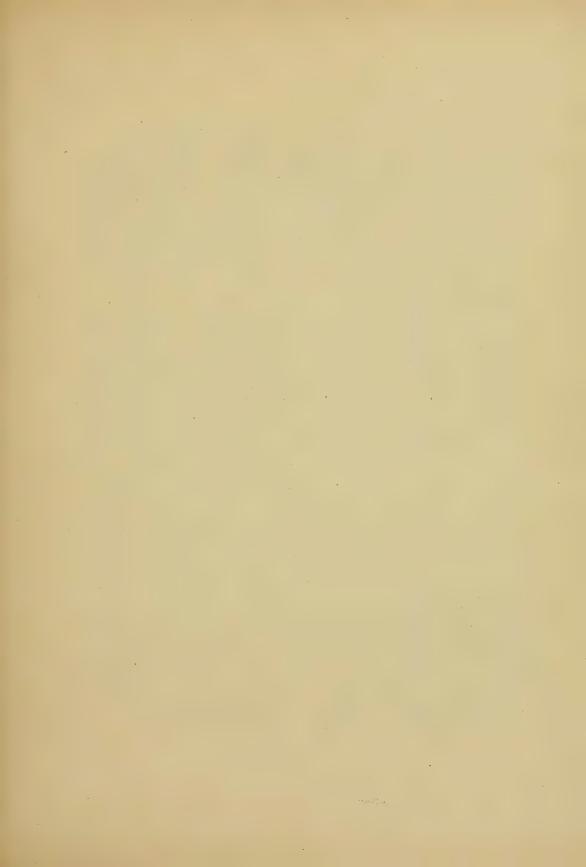
<sup>&</sup>lt;sup>3</sup> All these figures are enlarged about two diameters, except Fig. 9 and 12, which are about natural size.



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### PLATE IX.

Aster. obtusum.1 Fig. 1, var. D, loc. Lyme Regis.

Aster. stellare. Fig. 2, 3, figures reduced to about two thirds, loc. Tübingen. Aster. acceleratum.<sup>2</sup> Fig. 4 shows variety having the nearest approximation to Aster. stellare. The section is similar to that of Fig. 9, but is more involute. Loc. Semur.

Aster. Brooki. Fig. 5, 6, stout-whorled, broad-abdomened variety, approximating to Turneri, but with broader sides at the same age. Fig. 7, older stage of the same variety. Figures reduced to about two thirds. Loc. Lyme Regis.

Aster. Turneri. Fig. 8, 9, old specimen, figures reduced to about two thirds, loc. Semur.

Aster. Collenoti.3 Fig. 10, young, showing compressed form and acute abdomen. Fig. 10 a, b, the same more enlarged, but the figures fall short in depicting the acuteness of the abdomen, and by improper shading show a keel which has no existence. Fig. 11, young and older stage; the young are again too rounded, the outer whorl is however approximately accurate. Fig. 11 a, b, centre of same more enlarged, showing the involute form of even this early stage, but the front view is not sufficiently compressed. Loc. Semur.

Agas. Scipionis. Fig. 12, 13, lateral and sectional view of young, loc. Semur.

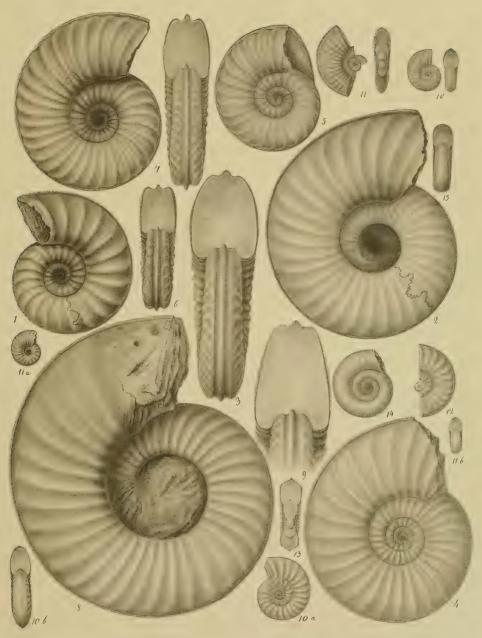
Agas. striaries. Fig. 14, 15, variety with flattened sides and broad abdomen, loc. Semur.

<sup>&</sup>lt;sup>1</sup> See Plate VIII. Fig. 4, 8.

<sup>&</sup>lt;sup>2</sup> The umbilical shoulders are not made abrupt enough in this figure, and the umbilicus is shallow as in Aster. stellare, instead of being deep as in this species. See Plate X. Fig. 3.

<sup>&</sup>lt;sup>3</sup> See Plate X. Fig. 10.

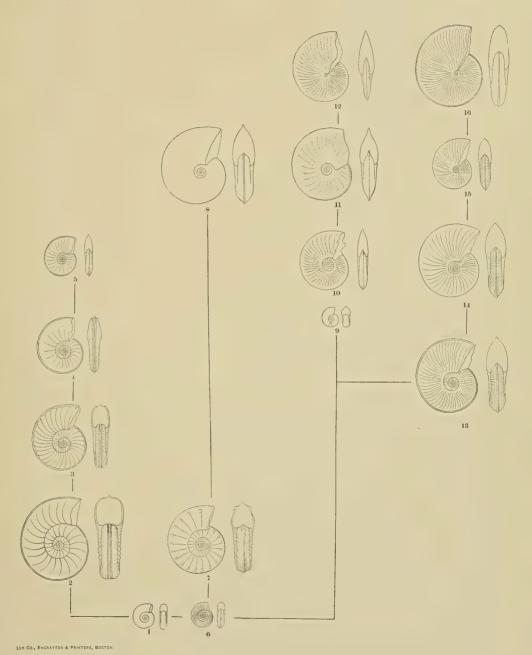
GENESIS OF THE ARIETIDAE. PLATE IX.



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## SUMMARY PLATE XIV.

The three preceding plates do not illustrate the biological relations of the Aietidæ as a whole with sufficient clearness, and this plate has been added for the purpose of supplying the deficiency. The series of Psiloceras has been placed in what may be deemed its true position, between the Plicatus stock and the Levis stock; otherwise, the arrangement is the same. The resemblances of the morphological equivalents in each series can be readily seen by following the forms along horizontal lines from left to right. The independence of the origin of these representative forms can be studied by following up the series in vertical lines, which represent descent. To a large extent, also, the more obvious differential characters which distinguish each series become appreciable by the same process.

Psil. planorbe, var. leve, Fig. 1; var. plicata, Fig. 2.

Schlot. catenata, Fig. 3, is the radical of this series.

Schlot. angulata, Fig. 24, is evidently a transition to the next species. The artist has exchanged Fig. 4 with Fig. 24.

Schlot. Charmassei, Fig. 5. The whorl is more involute, but the degenerate characters of compression in the whorls and shallowing of the abdominal channel begin to appear.

Schlot. Boucaultiana, Fig. 6. The involution has attained its maximum, and the degeneration of the pilæ and channel is well marked.

Wæh. curviornatum (sp. Wäh.), Fig. 7, is undoubtedly distinct from Schlot. angulata, and is one of the radicals of this series.

Wæh. haploptychum (sp. Wäh.), Fig. 28. The artist has exchanged Fig. 8 with Fig. 28. Wæh. toxophorum (sp. Wäh.), Fig. 9, is a degenerate shell, having compressed whorls, and pilæ crossing the abdomen, as in the proximate radical *Wæh. curviornatum*. It is, however, more involute.

Wæh. Emmerichi (sp. Wäh.), Fig. 10, shows a notably involute shell, with degenerate pilæ and compressed whorls.

Cal. tortile, Fig. 11, is the radical of this series.

Cal. carusense, Fig. 12, has similar young to that of tortile below.

Cal. Nodotianum, Fig. 13, is very similar to carusense, but with more compressed whorls and better developed pilæ.

Cal. cycloides (sp. Wäh.), Fig. 14, shows compressed degenerate whorls.

Cal. Castagnolai (sp. Wäh.), Fig. 15, is more degenerate than the last, but slightly more involute.

Cal. abnormilobatum (sp. Wäh.), Fig. 16, is a dwarfish and more degenerate form than Castagnolai, but has more involute whorls.

Cal. laqueum, Fig. 17, is an extreme form of this species, which approximates very closely to a true *spiratissimum*. This figure is therefore placed to the right, and under *Verm. spiratissimum*.

Verm. spiratissimum, Fig. 18, shows typical form, with but slight channels.

Verm. Conybeari, Fig. 19, shows normal untuberculated variety, with stout whorls and deep channels.

Verm. ophioides, Fig. 20, exhibits the tuberculated pilæ of this species.

Psil. aphanoptychum (sp. Wäh.), Fig. 21, is one of the Plicatus stock of Psiloceras.

Psil. Kammerkarense (sp. Wäh.), Fig. 22, shows the more involute and plicated form of this subseries.

Psil. mesogenos (sp. Wäh.), Fig. 23, is an involute shell belonging to the true Levis stock.\(^1\) Arn. semicostatum, Fig. 4. The figure represents the nearly full-grown shell; but if the keel were absent, the smooth whorls of the young would closely resemble the adult whorls of Psil. plunorbe, var. leve. The artist has exchanged Fig. 4 with Fig. 24.

Arn. Hartmanni, Fig. 25, exhibits young and adult characters like those of the preceding. Arn. tardecrescens, Fig. 26, belongs to another subseries of forms than that in which it is placed, but it serves to show that quadragonal whorled shells with channelled abdomens existed in this genus.

<sup>1</sup> Two subseries ought to have been shown here, but in trying to reduce the size of the plate the forms have been placed in the same line. A similar liberty has been taken with the subseries of Caloceras and Arnioceras, but this does not interfere with the truthful presentation of the general zoölogical relations of the forms.

Arn. Bodleyi, Fig. 27, shows a slightly degenerate compressed whorl, and is the terminal form of the subseries containing *Hartmanni*.

Arn. kridioides. Fig. 28 gives a view of the transition between Arnioceras and the lowest species of Coroniceras. The smooth young straight pilæ and divergent sides of the adult whorl are clearly shown. The artist has exchanged Fig. 8 with Fig. 28.

Cor. Sauzeanum. Fig. 29 shows the later nealogic and ephebolic stages, having the peculiar divergent sides, flattened abdomen, and prominent tubercles of a typical coroniceran form. The young, however, still retain the smooth aspect, indicating derivation from Arnioceras.

Cor. rotiforme. Fig. 30 represents a form similar to Cor. coronaries.

Cor. Lyra, Fig. 31. This is as a rule much smaller than rotiforme. The sides are more convergent, and the whorls more compressed and less numerous than in that species.

Cor. trigonatum, Fig. 32, exhibits the effects of the premature development of old age characters. Fig. 1 on the extreme right shows the dwarfed form of *Psil. planorbe*, var. *leve*, from which both the arnioceran as well as the agassiceran series may have been derived in Central Europe.

Agas. lævigatum. Fig. 33 shows the more compressed variety of this species.

Agas. striaries, Fig. 34. The striations were too fine to be represented.

Ast. obtusum. Fig. 2 shows the stouter variety with well marked channels with stout gibbous whorls and broad abdomen. This has young almost identical with the adults of the stout varieties of Agas. lavigatum.

Ast. Turneri. Fig. 36 shows typical variety, with flattened sides and deep channels. It is notably more involute than *obtusum*.

Ast. Brooki. Fig. 37 shows an extreme involute variety of this species, with very convergent sides and narrow abdomen. The channels are almost obliterated, and the keel very prominent.

Ast. Collenoti. Fig. 38 gives a view of this remarkable dwarfed form, in which degeneration of the pilæ and the channels and convergence of the sides have produced morphological equivalence with Oxyn. oxynotum and Guibali. The amount of the involution is greater than in any preceding species of the same series.

Agas. Scipionianum. Fig. 39 shows the stouter, heavily tuberculated variety, which has young almost identical with the stouter varieties of *Agas. striaries*.

Agas. Scipionis. Fig. 40 shows an aged specimen in the Museum of Comparative Zoology, with extremely involute whorls, but keel still prominent. The degeneration of the adult as regards the pilæ and form can, however, be inferred from this figure. The old of Scipionianum at the same age is much less changed, and does not exhibit increased involution of the whorls.

Oxyn. oxynotum, Fig. 41, 42. The first figure shows the young of a variety in which at an early stage there is close likeness to the young of Agas. striaries, and the adults of Agas. lævigatum.

Oxyn. Simpsoni. Fig. 43 shows the stouter form and slightly greater involution of the whorls in this species when compared with oxynotum.

Oxyn. Lymense. Fig. 44 shows the greater involution of whorls as compared with any preceding form of the same subseries, and the very acute degenerate whorl.

Oxyn. Greenoughi. Fig. 45 shows the stout form of the whorls better defined, and pilæ of this subseries as compared with the *oxynotum* subseries.

Oxyn. Lotharingum. Fig. 46 shows the smaller size of this species, and the degeneration of the pilæ. The involution of the whorls is, however, greater than in any preceding species.<sup>1</sup>

Oxyn. Oppeli. Fig. 47 shows the extremely involute form of the Middle Lias. The stout whorls indicate that no great amount of degeneration had taken place. It may have been a direct descendant of *Greenoughi*.

<sup>&</sup>lt;sup>1</sup> The extreme old age of this form is marked by decrease in the amount of involution of the whorl, and also by the loss of the prominent hollow keel.

